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V

# THE HEAD-CAPSULE AND MOUTH-PARTS OF DIPTERA

WITH TWENTY-FIVE PLATES

BY

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Contributions from the  
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THESIS

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## TABLE OF CONTENTS

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	PAGE
Introduction .....	7
Methods .....	8
Acknowledgments .....	9
Materials .....	9
Fixed Parts of the Head.....	13
Epicranial Suture .....	14
Fronto-clypeus .....	17
Tormae .....	19
Ptilinum .....	20
Labrum .....	20
Vertex .....	21
Compound Eyes and Ocelli.....	22
Occiput and Postgenae.....	23
Tentorium .....	26
Movable Parts of the Head.....	32
Antennae .....	33
Mandibles .....	34
Maxillae .....	36
Labium .....	41
Epipharynx and Hypopharynx.....	49
Summary .....	54
Bibliography .....	57
Explanation of Plates .....	61



## INTRODUCTION

The head and mouth-parts of Diptera offer a rich field for research. A number of excellent studies have been made by several investigators and they deserve careful consideration. A review of practically all the literature shows that a majority of the workers have examined only one or a few species. Meinert (1881) and Hansen (1883), however, studied a number of forms, but they were mostly specialized species; while an important study by Kellogg (1899) deals only with the families of the Nematocera. Becher (1882) is the only investigator who has studied a large series of generalized and specialized species. I have made a special effort to secure as many generalized and specialized species as possible, since it is highly desirable and essential in homologizing structures to have at hand a wide range of species.

Extensive studies have not heretofore been made, so far as I know, on the head-capsule; consequently the important relationship which exists between the mouth-parts and the head-capsule in generalized insects has not been traced in Diptera. This relationship is just as significant in ascertaining the correct interpretation of the mouth-parts of Diptera as it is in other orders. Its importance is illustrated by a study of the head and mouth-parts of the Thysanoptera (Peterson, 1915).

A review of the literature, Dimmock (1881) or Hansen (1883), discloses the many and varied interpretations that have been given to the mouth-parts of Diptera. To arrive at a correct interpretation of the fixed and movable parts of the head, the head-capsule and mouth-parts of all the species studied, irrespective of the established systematic position of the species, have been carefully compared with the head and mouth-parts of generalized insects. On the basis of this comparison, generalized, hypothetical types have been constructed for each fixed and movable part. Each hypothetical type is made up by an accumulation of all the generalized characters found among the Diptera, and should show an intermediate stage between generalized insects and Diptera. The use of such a hypothetical type is a great aid not only in showing how the dipterous type has been developed, but also in determining the homology of the parts.

The scope of this investigation makes it necessary to limit the discussions to the general subject of homology; consequently many details

of structure and other interesting modifications, shown in the figures but without direct bearing on the subject of homology, are necessarily disregarded. The fixed and various movable parts of the head are discussed separately, as developed from the hypothetical types, the discussions in every case proceeding from the generalized to the specialized.

All the general conclusions pertaining to the head and mouth-parts presented in the following pages are based entirely on a study of the species listed under "materials", unless otherwise stated. General statements in respect to the mouth-parts are true only for species having them well developed.

The names here adopted for the sclerites of the head and mouth-parts have been made to agree, so far as possible, with the terms now in common use for the same parts in generalized insects. The terms most commonly used thruout the literature for structures peculiar to this order have been adopted unless clearly unsuitable; and new terms have been applied only to structures described here for the first time and to parts to which the current names are inappropriate.

## METHODS

The greater part of this study was made from dried specimens that had been soaked from two to twenty-four hours in a 10% solution of potassium hydroxide. The sclerites of weakly chitinized forms show more clearly when they have been soaked for only a short time. After soaking, the heads were washed in distilled water to remove the potassium hydroxide and then preserved in 70% alcohol.

All dissections were made under a binocular microscope in 70% alcohol in deep watch-glasses or in carbol-aniline oil. Studies and figures were largely made from dissected parts in alcohol. Cleared preparations mounted in balsam were also found useful. In making such preparations the parts were dissected, stained, and cleared in carbol-aniline oil. This oil evaporates slowly, will mix readily with safranin or orange G dissolved in 95% alcohol, and will clear from any grade of alcohol above 50%. The staining of material with safranin before mounting proved to be very useful in differentiating the almost colorless parts of some species. When using aniline oil it is necessary to remove as much as possible of the oil before mounting, otherwise the balsam will eventually darken.

The material for sections was fixed with hot (80° C.) corrosive sublimate (saturated corrosive sublimate in 35% alcohol plus 2% of glacial acetic acid) for fifteen minutes to two hours. This was replaced by 70% alcohol containing a few drops of iodine, and the material was allowed to remain in this for twenty-four or more hours. Paraffin hav-

ing a melting point of 62–64 C. was a sufficiently firm medium in which to cut sections as thin as eight microns. Specimens stained in toto gave the best results. Delafield's haematoxylin required 24–48 hours, and borax carmine 3–7 days.

#### ACKNOWLEDGMENTS

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#### MATERIALS

The following list of insects includes all of the identified forms studied. The families of Diptera to which these species belong are arranged according to Aldrich's "Catalogue of North American Diptera". The generic and specific names of all but a few species may likewise be found in this catalog.

Aldrich lists fifty-nine families; of these, one or more representatives of fifty-three families have been studied. The following are not represented: Orphnephilidae, Acanthomeridae, Nemestrinidae, Apio-ceridae, Rhopalomeridae, and Nycteribiidae. The male and female of each species have been observed except in a few cases; in these the word "male" or "female" after the species name indicates which sex has been seen. Excepting one or two forms, the male and female have both been drawn if they were decidedly different. If the two sexes are similar, the figures were mostly made from the female. An asterisk before the name of a species indicates that this form has been embedded, sectioned, and studied. The figures following the various species refer to the drawings made of the same.



## DIPTERA

## Suborder Proboscidea

## Orthorrhapha-Nemocera.

Tipulidae.—\**Tipula bicornis* (Fig. 18, 95, 178, 277, 383, 384, 388, and 503), *Tipula cunctans*, *Tipula abdominalis*, *Limnobia immatura*, female (Fig. 93, 386, and 507), *Helobia punctipennis*, female (Fig. 385), *Trichocera bimacula*, male (Fig. 16, 78, 158, 200, 260, 311, 365, 499, and 500), *Geranomyia canadensis*, male (Fig. 382 and 506), *Ptychoptera rufocincta* (Fig. 15), and *Bittacomorpha clavipes*, male (Fig. 85 and 389).

Dixidae.—*Dixa clavata* (Fig. 19, 79, 163, 199, 262, 375, 387, 501, and 502), and *Dixa modesta* (Fig. 254).

Psychodidae.—*Psychoda albipennis* (Fig. 8, 82, 166, 202, 263, 318, 372, 529, and 530), and *Psychoda* sp.

Chironomidae.—*Chironomus ferugineovittatus* (Fig. 12, 88, 89, 152, 206, 207, 270, 312, 371, 531, and 532), *Culicoides sanguisugus* (Fig. 253, 265, and 521), and *Forcipomyia cilipes*.

Culicidae.—*Psorophora ciliata* (Fig. 10, 26, 96, 159, 210, 211, 251, 266, 373, 380, 381, 504, and 505), *Anopheles* sp., and \**Culex* sp.

Mycetophilidae.—*Sciara varians* (Fig. 17, 81, 150, 205, 267, 314, 360, 512, and 513), *Mycetobia divergens* (Fig. 7, 90, and 161), *Mycetophila punctata* (Fig. 11 and 87), and *Leia oblectabilis* (Fig. 368).

Cecidomyiidae.—*Rabdophaga strobiloides* (Fig. 6, 86, 170, 201, 268, 313, 367, 510, and 511), and *Cecidomyia* sp.

Bibionidae.—*Bibio femoratus* (Fig. 13, 14, 91, 92, 153, 154, 208, 264, 315, 364, 522, and 523), and *Bibio albipennis*.

Simuliidae.—*Simulium venustum*, female (Fig. 2, 77, 144, 204, 250, 258, 316, 366, 489, 497, and 498), *Simulium johannseni* (Fig. 3 and 252), *Simulium pecuarum*, and *Simulium jenningsi*.

Blepharoceridae.—*Bibiocephala elegantula* (Fig. 4, 5, 76, 83, 155, 156, 203, 256, 269, 399, 526, and 527), and *Blepharocera* sp.

Rhyphidae.—*Rhyphus punctatus* (Fig. 9, 80, 157, 209, 261, 321, 374, 508, and 509).

## Orthorrhapha-Brachycera.

Stratiomyiidae.—*Stratiomyia apicula* (Fig. 27, 28, 104, 160, 213, 273, 331, 395, 396, 545, and 546), and *Stratiomyia meigeni*.

Tabanidae.—*Tabanus giganteus* (Fig. 20, 21, 74, 75, 142, 143, 214, 255, 259, 283, 317, 390–392, and 494–496), *Tabanus sulcifrons*, *Tabanus atratus*, *Tabanus trimaculata*, and *Chrysops striatus*.

Leptidae.—*Leptis vertebrata* (Fig. 34, 35, 103, 145, 218, 275, 323, 369,

- 370, 520, and 525), *Chrysopila proxima*, *Chrysopila thoracica*, *Chrysopila quadrata*, and *Chrysopila velutina*.
- Cyrtidae.—*Oncodes costatus* (Fig. 53, 105, 109, 220, 486, and 487), *Eulonchus tristis* (Fig. 284a, 364a, 425a, 425b, and 543), and *Pterodontia flavipes*.
- Bombyliidae.—*Exoprosopa fasciata* (Fig. 29, 98, 162, 216, 285, 361-426-429, 549, and 550), *Systoechus vulgaris*, *Lepidophora* sp., and *Bombylius major* (Fig. 482).
- Therevidae.—*Psilocephala haemorrhoidalis* (Fig. 33, 36, 100, 173, 281, 324, 402, 403, 533, and 534).
- Scenopinidae.—*Scenopinus fenestralis* (Fig. 41, 42, 107, 149, 219, 282, 325, 400, 401, 537, and 538).
- Mydidae.—*Mydas clavatus* (Fig. 30, 99, 146, 212, 271, 319, 397, 398, 535, and 536).
- Asilidae.—*Promachus vertebratus* (Fig. 22, 84, 147, 148, 217, 276, 322, 376-379, and 517-519), *Asilus notatus*, and *Deromyia umbrina*.
- Dolichopodidae.—*Dolichopus bifRACTUS* (Fig. 43, 112, 168, 226, 284, 432-434, 524, and 528), *Dolichopus* sp. (Fig. 108), *Psilopodinus siphon*, and *Sympycnus lineatus*.
- Empididae.—*\*Empis clausa* (Fig. 26, 40, 97, 164, 215, 274, 352, 421-423, 547, and 548), *Rhamphomyia glabra* (Fig. 424 and 425), and *Euhabus* sp.
- Lonchopteridae.—*Lonchoptera lutea* (Fig. 37, 102, 177, 223, 280, 320, 406-408, 539, and 541).
- Phoridae.—*Aphiochaeta agarici* (Fig. 31, 111, 174, 224, 278, 335, 393, 394, 540, and 544), *Metopina* sp., and *Dohrniphora concinna*.
- Cyclorrhapha-Athericera.
- Platypezidae.—*Platypeza velutina* (Fig. 32, 110, 165, 222, 272, 326, 415, 416, 542, and 542a).
- Pipunculidae.—*Pipunculus cingulatus* (Fig. 38, 39, 106, 151, 243, 279, 327, 435, 436, 561, and 562).
- Syrphidae.—*Eristalis tenax* (Fig. 23-25, 113, 167, 232, 286, 328, 441-443, 587, and 588), *Syrpitta pipiens*, and *\*Allograpta obliqua*.
- Conopidae.—*Conops brachyrhynchus* (Fig. 67, 117, 186, 221, 305, 356, 417-420, 591, and 592), *Stylogaster biannulata* (Fig. 359), and *Physocephala tibialis*.
- Cyclorrhapha-Calypttratae.
- Oestridae.—*Gastrophilus equi* (Fig. 54, 138, 239, and 490-492).
- Tachinidae.—*Archytas analis* (Fig. 68, 124, 197, 247, 309, 353, 468, 469, 604, and 605), *Siphona geniculata* (Fig. 355 and 458),

- Gonia capitata*, *Ocyptera carolinae*, and *Gymnosoma fuliginosa*.  
Dexiidae.—*Thelaira leucozona* (Fig. 65, 128, 196, 230, 301, 346, 473, 474, 595, and 596).  
Sarcophagidae.—*Sarcophaga haemorrhoidalis* (Fig. 66, 130, 191, 244, 310, 350, 477, 478, 602, and 603).  
Muscidae.—\**Musca domestica* (Fig. 71, 72, 133, 194, 242, 304, 351, 465–467, 600, and 601), *Calliphora vomitoria* (Fig. 484 and 485), \**Stomoxys calcitrans* (Fig. 354, 479, 480, and 599), *Myiospila mediatubunda* (Fig. 120), *Pollenia rudis*, *Lucilia caesar*, and *Calliphora erythrocephala*.  
Anthomyiidae.—*Hydrotaea dentipes* (Fig. 69, 70, 127, 195, 241, 308, 349, 475, 476, 597, and 598), *Lispa nasoni* (Fig. 116 and 481), *Dexiopsis lacteipennis*, *Coenosia aurifrons*, and *Chortophila* sp.  
Cyclorrhapha-Acalyptratae.  
Scatophagidae.—*Scatophaga furcata* (Fig. 62, 135, 193, 246, 307, 357, 470–472, 593, and 594).  
Heteroneuridae.—*Heteroneura flaviseta* (Fig. 49, 126, 176, 229, 298, 340, 459, 460, 589, and 590).  
Helomyzidae.—*Oecotha fenestralis* (Fig. 48, 137, 192, 227, 290, 332, 452, 453, 580, and 581).  
Borboridae.—*Borborus equinus* (Fig. 63, 136, 188, 231, 294, 342, 437, 438, and 565–567), *Limosina ferruginata*, and *Sphaerocera pusilla*.  
Phycodromidae.—*Coelopa vanduzeei* (Fig. 58, 121, 182, 288, 337, 448, 449, 559, and 560).  
Sciomyzidae.—*Tetanocera plumosa* (Fig. 55, 119, 180, 225, 302, 344, 463, 464, 584, and 586), and *Sepedon fuscipennis*.  
Sapromyzidae.—*Sapromyza vulgaris* (Fig. 60, 115, 171, 248, 289, 329, 409, 410, 553, and 554), *Sapromyza bispina*, *Minettia lupulina*, and *Lonchaea polita*.  
Ortaliidae.—*Chrysomya demandata* (Fig. 64, 134, 181, 245, 295, 341, 456, 457, 557, and 558), *Tritoxa incurva*, *Chaetopsis aenea*, *Camptoneura picta*, *Pyrgota* sp., and *Eumetopia* sp.  
Trypetidae.—*Euaresta aequalis* (Fig. 61, 131, 175, 240, 292, 347, 413, 414, 572, and 573), *Trypeta alba*, and *Straussia longipennis*.  
Micropezidae.—*Calobata univitta* (Fig. 44, 114, 183, 236, 296, 348, 446, 447, 551, and 552).  
Sepsidae.—*Sepsis violacea* (Fig. 46, 118, 184, 234, 287, 334, 439, 440, 582, and 583), and *Prochyliza xanthostoma*.  
Psilidae.—*Loxocera pectoralis* (Fig. 59, 123, 169, 235, 300, 339, 461, 462, 570, and 571).



Diopsidae.—*Sphyracephala bicornis* (Fig. 52, 94, 190, 293, 338, 450, 451, and 585).

Ephydriidae.—*Ochthera mantis* (Fig. 56, 101, 187, 237, 297, 336, 444, 445, 483, and 574–577), *Paralimna appendiculata*, and *Parydra bituberculata*.

Oscinidae.—*Chloropisca glabra* (Fig. 51, 132, 189, 306, 345, 430, 431, 555, and 556), *Siphonella abdominalis*, and *Hippelates flavipes*.

Drosophilidae.—*Drosophila ampelophila* (Fig. 45, 125, 172, 238, 291, 343, 454, 455, 563, and 564).

Geomyzidae.—*Chyromya concolor* (Fig. 50, 122, 179, 233, 299, 333, 411, 412, 568, and 569).

Agromyzidae.—*Desmometopa latipes* (Fig. 47, 129, 185, 228, 303, 330, 404, 405, 578, and 579).

#### Suborder Eproboscidea

Hippoboscidae.—*Olfersia ardeae* (Fig. 57, 139, 198, 249, 358, 488, and 606), and *Melophagus ovinus*.

#### ORTHOPTERA

*Periplaneta orientalis* (Fig. 514).

*Melanoplus differentialis* (Fig. 515).

*Gryllus pennsylvanicus* (Fig. 516).

Hypothetical and typical figures (Fig. 1, 73, 140, 141, 199h, 256h, 257, 362, 363, and 493).

#### FIXED PARTS OF THE HEAD

A hypothetical head-capsule of Diptera (Fig. 1) has a dorso-ventral extension. The epicranial suture (e.s) is present on the meson, and extends from the occipital foramen (o.f) to a point on the cephalic aspect ventrad of the antennae. At this point it bifurcates and the two arms continue to the invaginations of the anterior arms of the tentorium (i.a), which are situated at the dorso-lateral angles of the clypeus (c). The three unpaired sclerites included within, or ventrad of, the fork of the epicranial suture are the front (fr), clypeus (c), and labrum (l). The fronto-clypeal suture is represented by a dotted line in the figure. The vertex (v) includes all of the dorsal and cephalic aspects of the epicranium except the front (fr), while the genae (ge) are the regions of the vertex ventrad and mesad of the compound eyes. Two large compound eyes (c.e) cover the lateral portions of the cephalic aspect. Three ocelli (oc) are situated on the vertex. The occiput (occ) and postgenae (po) constitute the caudal aspect of the head-capsule.

The tentorium (t) of the hypothetical head-capsule has three pairs of invaginations, homologous with the invaginations in generalized insects. The invaginations of the posterior arms (i.p) of the tentorium are situated ventrad of the occipital foramen at the distal ends of chitinized thickenings. The invaginations of the dorsal arms of the tentorium (i.d) are on the cephalic aspect near the antennae and adjacent to the epicranial suture, while the invaginations of the anterior arms of the tentorium (i.a) are situated in the epicranial suture and adjacent to the dorso-lateral angles of the clypeus.

The heads of all Diptera have a dorso-ventral extension, and in this respect resemble the heads of many generalized insects. Some of the primary sutures, sclerites, and invaginations of the head of such an insect are present in a number of the Nematocera and in a few of the Brachycera. The hypothetical head-capsule has been constructed from these forms. The heads of the Acalyptratae and the Calyptratae are highly specialized by the modification, union, reduction, and membranous development of parts, consequently very few if any primary characters remain which can be homologized with these structures. The membranous development of areas has been the most important process of specialization. The stippled areas on the figures show the extent of the membrane. The various parts of the head-capsule are discussed individually and in the order in which they were described for the hypothetical type. The heads of Diptera naturally fall into two groups according to the presence or absence of a frontal suture (fr.s) and a ptilinum (pt). The forms without a frontal suture are the more generalized.

*Epicranial Suture.*—The epicranial suture of all insects originates in the embryo. The stem of the suture on the dorso-meson represents the line along which the paired parts of the head meet, while the arms of the suture (a.e.s) represent the place of contact between the paired sclerites of the head and the mesal unpaired sclerites. The epicranial suture (e.s) of a hypothetical dipterous head corresponds to the above description, and is homologous with the epicranial suture found in the heads of generalized immature and adult insects of the more common orders. The following examples illustrate the homology between the hypothetical type and other insects. The epicranial suture in the larva of *Corydalis*, and in the generalized larvae of the Coleoptera, Lepidoptera, and certain Hymenoptera, is complete, and its two arms join with the margins of the clypeus, as in the hypothetical type.

The epicranial suture of the adults of the Orthoptera, Hemiptera, and Hymenoptera also resembles this suture in the hypothetical head, providing the following interpretation of this suture is accepted. In

the adults of *Gryllus* and *Periplaneta* it is complete and similar to that of *Corydalis* except that a small portion of each arm is wanting about the antennae and the lateral ocelli. The ventral ends of the arms are commonly called the fronto-genal sutures, and they join with the clypeus as in *Corydalis*. All insects that have a sucking type of mouth, such as the Hemiptera and Hymenoptera, usually show no signs of the stem of the epicranial suture. The arms, however, are distinct and form the lateral and dorsal boundaries of the large mesal piece commonly called the clypeus. A large number of the Diptera possess an epicranial suture which closely resembles that of the Hemiptera and the Hymenoptera. On the basis of the above interpretation of the epicranial suture it has been possible to homologize the sutures and sclerites, and the invaginations of the tentorium on the cephalic aspect. No other interpretation gave satisfactory results.

The epicranial suture (e.s) in *Mycetophila* (Fig. 11) is complete and closely resembles the hypothetical type. In *Leia* it closely resembles that of *Mycetophila* except for the stem of the suture, which is wanting dorsad of the median ocellus. The stem of the epicranial suture in *Psorophora* (Fig. 10 and 26) and *Chironomus* (Fig. 12) is represented by a distinct suture in a deep fold on the meson. Other forms, such as *Rhabdophaga* (Fig. 6), *Mycetobia* (Fig. 7), and *Tabanus* (Fig. 20), show depressions or thickenings along the meson. These marks may have no significance. Outside of the above-mentioned forms, the stem of the epicranial suture is wanting.

The arms of the epicranial suture (a.e.s) are present in many Diptera. This is the case in all but a few of the Nematocera, in a majority of the Brachycera, and in many of the families of the Cyclorrhapha. These resemble, therefore, the adults of the Hemiptera and Hymenoptera. The arms are present as definite sutures between two chitinized areas in *Tabanus* (Fig. 20 and 21) and *Leptis* (Fig. 35), and in the female of *Simulium* (Fig. 2). The epicranial suture is apparently wanting in the male of *Simulium* (Fig. 3) unless the lateral margins of the convex area represent it. In many genera the epicranial suture is represented by the edge of a chitinized sclerite. This is the case in *Chironomus* (Fig. 12), *Trichocera* (Fig. 16), *Psorophora* (Fig. 10), *Mycetobia* (Fig. 7), and *Dixa* (Fig. 19). The vertex in the genera just named is membranous between the antennal fossae and the epicranial suture. *Sciara* (Fig. 17), *Rhabdophaga* (Fig. 6), *Bibiocephala* (Fig. 4 and 5), and possibly *Rhyphus* (Fig. 9) and *Bibio* (Fig. 14), have the arms of the epicranial suture represented by the chitinized margin of the vertex, which is adjacent to the membranous portion of the fronto-clypeus. The location of the invaginations of the arms of the



tentorium usually helps to determine the location of the epicranial suture. In *Ptychoptera* (Fig. 15) the invaginations of the anterior arms of the tentorium are located in the distinct V-shaped depression on the chitinized area ventrad of the antennae. Undoubtedly this depression marks the position of the epicranial suture. *Tipula* (Fig. 18) has a very specialized head and shows no epicranial suture or tentorium.

Only the arms of the epicranial sutures are present in the *Brachycera*. On the whole these sutures are not as well developed in the *Brachycera* as in the *Nematocera*. When present (a.e.s) they are long and slit-like in all the genera except *Tabanus*. This condition is due to the fusion of the invaginations of the dorsal arms and the anterior arms of the tentorium along each suture. The arms of this suture in *Tabanus* (Fig. 20 and 21) unite the invaginations on each lateral half of the head, but they are not decidedly slit-like.

The arms of the epicranial suture (a.e.s) in *Tabanus* (Fig. 20) have the usual inverted-u shape and their ventral ends terminate at the ventral margin of the head. The arms are indistinct ventrad of the invaginations of the anterior arms of the tentorium. The invaginations (i.a) in *Promachus* (Fig. 22) are slit-like and situated near the ventrolateral angles of the compound eyes. The epicranial suture is wanting dorsad and ventrad of the invaginations of the anterior arms, and in this respect *Promachus* differs from *Leptis* and *Tabanus*. From *Leptis* (Fig. 35) it is possible to homologize the arms of the epicranial suture of all the *Brachycera* and those of the *Cyclorrhapha*. The arms of the suture in *Leptis* are long and slit-like and coincide with the invaginations of the tentorium on the cephalic aspect of the head. They extend dorsad from the ventral margin of the head to a point ventrad of the antennae, where they unite and enclose a convex mesal area called the fronto-clypeus (fr.c). This suture (a.e.s) in *Platypeza* (Fig. 32) closely resembles that of *Leptis*. The dorsal ends of the arms of the epicranial suture are wanting in *Psilocephala* (Fig. 36), *Mydas* (Fig. 30), *Exoprosopa* (Fig. 29), *Eristalis* (Fig. 23 and 25), and *Scenopinus* (Fig. 41 and 42), and in other forms. *Scenopinus* shows a striking variation in that the vertex is membranous between the antennae and the fronto-clypeus, and no epicranial suture can be traced thru the membrane. *Stratiomyia* (Fig. 27) shows a unique development of the slits in that they extend mesad rather than dorsad. This condition is undoubtedly a secondary development. The epicranial suture of *Lonchoptera*, *Aphiochaeta*, *Pipunculus*, and *Empis* is discussed under fronto-clypeus.

No epicranial suture or slit-like invaginations are present in any dipteran that has a frontal suture (fr.s) or a ptilinum (pt). Since

the tentorium on the cephalic aspect and the arms of the epicranial suture are usually closely associated in insects, there is every reason to believe that the tentorial thickenings (t.th) mark the course of the suture (a.e.s). Furthermore, the location of the thickenings of the tentorium is very similar to the location of the slit-like invaginations of *Leptis* (Fig. 35). These thickenings (t.th) have been considered as marking the course of the arms of the epicranial suture. The extent of the tentorial thickenings varies considerably, as shown in the figures. In *Tetanocera* (Fig. 55), *Chloropisca* (Fig. 51), *Heteroneura* (Fig. 49), and others, the tentorial thickenings extend to the antennal fossae (a.f). No sutures are present between the dorsal ends of these thickenings.

*Fronto-clypeus*.—The front (fr) and clypeus (c) of all insects are unpaired sclerites located between the arms of the epicranial suture (a.e.s). The labrum (1) is also an unpaired sclerite attached typically to the ventral margin of the clypeus. These three sclerites and their parts are not always distinguishable. This is particularly true of the front and clypeus in Diptera. The dotted, transverse line uniting the invaginations of the anterior arms of the tentorium (i.a) in the hypothetical head indicates the position of the fronto-clypeal suture. In a few of the *Orthorrhapha*, suture-like marks, depressions, or thickenings extend across the chitinized portion of the fronto-clypeus. These marks in *Chironomus* (Fig. 12), *Mycetophila* (Fig. 11), and *Rhabdophaga* (Fig. 6) resemble the fronto-clypeal suture as indicated in the hypothetical type. It is possible that they are remnants of this suture. Excepting in the forms named, one can not be sure of the presence of a fronto-clypeal suture; consequently the entire area between the labrum and the arms of the epicranial suture has been designated as the fronto-clypeus (fr.c). The absence of the fronto-clypeal suture in Diptera is not unusual, since it is wanting in many generalized insects. For those who may wish to divide the fronto-clypeus into two areas, the dorsal half would be the front and the ventral half the clypeus. A large portion of the fronto-clypeus is membranous in *Rhabdophaga* (Fig. 6), *Rhyphus* (Fig. 9), and *Sciara* (Fig. 17), and the chitinized part is greatly reduced. The variations found in the *Nematocera* are represented in the figures.

The *Brachycera* show two lines of development in the modification of the area enclosed by the arms of the epicranial suture. Both of these started from a form which possessed an epicranial suture similar to that of *Leptis* (Fig. 35). The line of development seen in *Psilocephala*, *Platypeza*, *Scenopinus*, *Lonchoptera*, and *Aphiochaeta* is considered first. The chitinized fronto-clypeus of *Leptis* resembles the fronto-clypeus of a number of the *Nematocera*, as *Sciara* (Fig. 17). From this simple

condition it is possible to develop the type of fronto-clypeus found in *Psilocephala* (Fig. 33 and 36). This came about by a membranous development on the meson and on the lateral margins of the fronto-clypeus and the loss of the arms of the epicranial suture directly ventrad of the antennae. The membranous development of the fronto-clypeus of *Platypeza* (Fig. 32) resembles that of *Psilocephala*. *Scenopinus* (Fig. 41 and 42) belongs to this same line, but in this genus the antennae are adjacent to the fronto-clypeus and no portion of the chitinized vertex exists between them. The form of the chitinized portion of the fronto-clypeus resembles closely that of *Platypeza* (Fig. 32). *Aphiochaeta* (Fig. 31) and *Lonchoptera* (Fig. 37) apparently belong to this same series. If such is the case, the arms of the epicranial suture do not project dorsad but are represented by the nearly straight ventral margin of the cephalic aspect. This condition must have come about by the straightening out of the usual u-shaped depression, and the chitinized part of the fronto-clypeus is located ventrad of the margin of the head. The tentorial thickenings along the ventral margin of the head in *Lonchoptera* afford evidence favorable to the above interpretation. A similar type of development occurs in *Bibio* (Fig. 14), in which the invaginations for the anterior arms of the tentorium are located on the ventral margin of the head-capsule latero-ventrad of the antennal fossae. All the other *Brachycera* and *Cyclorrhapha* figured, show the presence of sclerites designated as the tormae and located ventrad of the fronto-clypeus, and this fact places them in the line of specialization which leads toward a muscid type.

The fronto-clypeus (fr. c) is present in all *Diptera* and constitutes a prominent portion of the head-capsule. In *Tabanus* (Fig. 20 and 21) the fronto-clypeus is the entire area ventrad of the epicranial suture and outside of the tormae and the labrum. The sutures separating the fronto-clypeus from the genae (ge) are very indistinct. No arms of the epicranial suture are present in *Promachus* (Fig. 22), *Empis* (Fig. 40), and *Pipunculus* (Fig. 38); consequently the dorsal extent of the fronto-clypeus can not be determined, and the area ventrad of the antennae is considered as the fronto-clypeus. The fronto-clypeus of *Mydas* (Fig. 30) resembles that of *Leptis*, and from a type similar to *Mydas* it is possible to develop the fronto-clypeus of *Exoprosopa* (Fig. 29), *Eristalis* (Fig. 25), and probably *Stratiomyia* (Fig. 27). The fronto-clypeus of *Mydas* closely resembles that of the *Acalyptratae* and the *Calypttratae*, as will be seen by comparing *Mydas* with *Tetanocera* (Fig. 55), *Chloropiscea* (Fig. 51), *Chyromya* (Fig. 50), and *Musca* (Fig. 72). It is not a completely chitinized area in all of the genera studied, and the significance of this mesal membranous area in *Sepsis*, *Oecotheca*, and *Calobata* has been suggested in the discussion on the ptilinum.



*Tormae*.—The tormae (to) in generalized insects are chitinized pieces which belong to the lateral portions of the epipharynx in the region of the clypeo-labral suture and connect with the clypeus or labrum at the lateral ends of the suture. These are well illustrated in such Orthoptera as *Periplaneta* (Fig. 514), *Melanoplus* (Fig. 515), and *Gryllus* (Fig. 516).

The tormae of generalized Diptera also connect with the inner surface of the ventral portion of the fronto-clypeus. They are not well-developed structures or readily distinguishable from the fronto-clypeus in a number of species of the Nematocera. This seems to be due to the decidedly convex nature of the fronto-clypeus and the close proximity of its lateral portions to the lateral margins of the epipharynx. The tormae of *Leptis* (Fig. 520), *Psilocephala* (Fig. 36 and 533), *Scenopinus* (Fig. 41 and 538), *Aphiochaeta* (Fig. 31 and 544) *Lonchoptera* (Fig. 37 and 539), and *Platypeza* (Fig. 32 and 543) connect with the fronto-clypeus and thus resemble the Nematocera and the hypothetical type. In *Tabanus*, the tormae (Fig. 494) resemble the above genera in their connection with the fronto-clypeus, but they have been enlarged ventrad until they are exposed between the clypeus and the labrum (Fig. 20 and 494). The exposed portions of the tormae resemble two small, triangular sclerites with their pointed ends meeting on the meson. This condition is not unusual since they resemble closely the exposed portions of the tormae located at the lateral ends of the clypeo-labral suture in *Gryllus* (Fig. 516). *Simulium* (Fig. 2 and 489) also shows exposed portions of the tormae at the ventro-lateral angles of the fronto-clypeus (fr. c).

The inverted chitinized V-shaped piece ventrad of the fronto-clypeus in *Mydas* (Fig. 30) has undoubtedly been derived from the fusion of the tormae of some form resembling *Tabanus* (Fig. 20). The tormae are adjacent to the fronto-clypeus in *Mydas*, but they are not connected with the same as in *Tabanus*. From the type of tormae found in *Mydas* it is possible to develop the tormae of all other genera. The tormae vary in shape and position as seen in the cephalic views of the head. In *Exoprosopa* (Fig. 29), *Eristalis* (Fig. 25), and *Stratiomyia* (Fig. 27) they show a striking development in that they are located within deep emarginations of the ventral margin of the fronto-clypeus. The tormae of *Empis* (Fig. 40) closely resemble those of *Mydas* and belong to the same line of development. In *Pipunculus* (Fig. 38) the tormae resemble the fronto-clypeus of *Sciara* (Fig. 17), but as a matter of fact the fronto-clypeus is the area ventrad of the antennae, as shown by the location (Fig. 151) of the dorsal arms of the tentorium (d. a.). The tormae of the *Acalyptratae* are usually crescent-shape, while in the *Calyptratae* they resemble the type found in *Mydas*.

*Ptilinum*.—A deep, inverted U-shaped groove is present in the heads of all the Calyptratae and the Acalyptratae dorsad of the antennae. This groove is called the frontal suture (fr. s) and marks the line of invagination of the large membranous pouch, the ptilinum (pt). In Sphyracephala (Fig. 52) the frontal suture is V-shaped, owing to the peculiar development of the head. The extent of the invagination of the ptilinum (pt) is indicated by a dot-and-dash line in the drawings of the cephalic and lateral views of the head-capsule.

The origin of the ptilinum has been a mystery to morphologists. After a careful examination of the heads of the Brachycera and the Cyclorrhapha, no definite data were found which would throw any light on its origin. A few forms, however, suggested a possible way in which it might have been developed. The frontal suture and the ptilinum are comparatively small in Tetanocera (Fig. 55), Sapromyza (Fig. 60), Conops (Fig. 67), Ochthera (Fig. 56), and Chloropisca (Fig. 51). These genera gave no clue to the early stages of its development unless the thinly chitinized condition of the fronto-clypeus of Chloropisca has some significance. It seems evident that the frontal suture was once a membranous area which became invaginated to form a membranous pouch or ptilinum. If this is the case, the mesal membranous area of the fronto-clypeus of Sepsis (Fig. 46), Oecothoa (Fig. 48), Calobata (Fig. 44), and Desmometopa (Fig. 47) would be very significant. The ptilinum might possibly have originated from some form similar to Scenopinus (Fig. 41), in which the ventral margin of the chitinized vertex is located dorsad and laterad of the antennae. It seems quite possible that the membrane along this margin became invaginated in the early stages of the development of the ptilinum. The above conjectures may or may not be correct. A real solution of the problem will undoubtedly require a careful study of the pupal development.

*Labrum*.—The labrum (l) of a hypothetical dipterous head (Fig. 1, 140, and 493) is a distinct, chitinized, tongue-like structure connected with the ventral margin of the clypeus. The shape and size of the labrum are identical with the shape and size of the epipharynx, which is located on its caudal aspect. The labrum (l) and epipharynx (ep) are joined together by a membrane along their lateral margins. These two structures thus act as one organ and they have rightly been called the labrum-epipharynx (l. ep). The above relation of the labrum to the epipharynx and the fronto-clypeus resembles that in the Orthoptera.

In a general way the labrum of all the genera studied resembles the hypothetical type described above. It varies, however, in shape and in degree of chitinization. In Promachus (Fig. 22), in Psorophora (Fig. 10 and 26), and in the female of Tabanus (Fig. 20) it is completely



chitinized and separated from the fronto-clypeus by a suture. In all other genera there is a distinct membranous area present between the fronto-clypeus and the labrum. This area is very extensive in the *Cyclorrhapha* and includes the ectal exposure of the tormae. The labrum of a few scattered genera, such as *Rhabdophaga* (Fig. 6), *Mycetobia* (Fig. 7), *Chironomus* (Fig. 12), *Scenopinus* (Fig. 41), and others, is completely membranous, while in still others it is nearly so, as in *Mydas* (Fig. 30). The figures of the cephalic aspect of the head and the lateral views of the epipharynx and the hypopharynx show the shape and extent of the chitinization of the labrum.

The labrum of *Dixa* (Fig. 501), *Trichocera* (Fig. 499), *Sciara* (Fig. 513), *Bibio* (Fig. 523), *Simulium* (Fig. 497), *Culicoides* (Fig. 521), *Tabanus* (Fig. 20), and *Dolichopus* (Fig. 528) is distinctly separated from the epipharynx (ep) by a membrane. This condition is best seen in a lateral view. A majority of the forms studied have little or no membrane between the labrum and epipharynx. This is particularly true of the *Cyclorrhapha*. The surface of the labrum of all *Diptera* is more or less convex. In a large number of the genera the convexity is very decided and of such a nature as to surround the cephalic and lateral aspects of the epipharynx. The epipharynx in these forms can only be seen in a caudal view. In the *Calypttratae*, the labrum and epipharynx are firmly united in one piece.

The labrum of *Simulium* (Fig. 2 and 489) is unique in that the chitinized part consists of a narrow mesal piece which bifurcates at its distal end. These bifurcations give rise to special small hook-like structures (h) which have been incorrectly interpreted as mandibles (Smith, 1890). The labrum and epipharynx of *Psorophora* (Fig. 504) fit together very closely. By careful dissection they may be separated, as seen in the drawing. So far as observed, no membrane is present between them. The proximal end of the labrum is crook-like in form, and muscles connect with this portion.

*Vertex*.—The vertex (v) of a hypothetical head (Fig. 1) consists of the paired continuous areas on the cephalic aspect of the epicranium. It is interpreted as including all the cephalic and dorsal aspects of the epicranium except the front. In a number of the *Diptera*, as heretofore described, the stem of the epicranial suture (s. e. s) is present and marks the line of fusion of the two halves of the vertex, upon which the ocelli and the antennae are located. The shape and size of the chitinized portion of the vertex is largely determined by the size of the compound eyes, the location and extent of the membranous area about the base of the antennae, and the location of the arms of the epicranial suture. The variations in the size and shape of the vertex are shown in the figures of the cephalic aspect of the head.

The region of the vertex ventrad and mesad of each compound eye is a gena. The size of the genae (ge) is dependent upon the location of the compound eyes and the ventral extension of the head-capsule. The figures show considerable variation in these respects.

*Compound Eyes and Ocelli.*—The compound eyes (c. e) of a hypothetical head are large oval structures located on the cephalo-lateral aspects of the head-capsule. They cover from one-half to two-thirds of the entire cephalic aspect and their caudal margins are adjacent to the lateral margins of the head. The compound eyes of a majority of the Diptera resemble in general the hypothetical type. The shape and size vary considerably with the different species. Variations are most prevalent in the families of the Orthorrhapha. This variability agrees with the decided variability of other parts. In such genera as *Tipula* (Fig. 95), *Psorophora* (Fig. 96), and *Limnobia* (Fig. 93) the compound eyes are exceptional in that they extend onto the caudal aspect of the head. The variations in shape are well illustrated by the numerous figures.

The compound eyes show secondary characters in a greater number of species than any other fixed or movable part. This sexual variation is most prevalent among the Nematocera and the Brachycera, and was not observed in the Acalyptratae. Among the Calyptratae, slight differences occur in *Musca* (Fig. 71 and 72) and *Hydrotaea* (Fig. 69 and 70). When sexual variation occurs, the eyes of the male are larger than those of the female, and they are usually adjacent along a portion of their mesal margins. Such species are said to be holoptic; while all the females, and some of the males, having the eyes distinctly separated, are dichoptic. The extent of the holoptic condition depends upon the size of the eyes and the location of the antennal fossae, as in *Simulium* (Fig. 2 and 3) and *Biblio* (Fig. 13 and 14). In the male of *Biblio* the compound eyes are adjacent along their mesal margin and the antennal fossae (a. f) are located ventrad of the eyes. The extent and nature of the sexual variation is shown in the figures. Except in the case of *Empis* the heads of the male and female have both been drawn when decided differences are present.

The facets or ommatidia of the compound eyes vary in number, form, and size thruout the order. In the Nematocera they are usually large and not as closely compacted as in the Cyclorrhapha. An interesting variation occurs in the male of *Simulium*, the facets (fa) of the ventral half of the eye being smaller than those of the dorsal half. This difference is also found in the female of *Bibiocephala* (Fig. 5). In the male of *Biblio* (Fig. 154) the facets (fa) in the ventro-caudal portions of the eyes are smaller than the others. The compound eyes of *Bibiocephala* and *Blepharocera* are divided into a dorsal and a ventral por-

tion by a transverse constriction (ch), where the ommatidia are wanting. This constriction is also present in *Bibio*, but in this form it is confined to the caudo-ventral portion of the eye.

The drawings of the lateral aspects of some heads show a line of dashes or a solid line around the margins of the compound eyes. This line indicates the extent of the infolding of the head-capsule adjacent to the compound eye. This infolding, or ocular sclerite (o.s), is figured only for those species in which it is closely related to the external markings found on the caudal aspect dorsad of the occipital foramen. The influence of this invaginated edge will be more fully discussed later.

The three ocelli (oc) of the hypothetical head-capsule (Fig. 1) are arranged in the form of a triangle and located on the cephalo-dorsal aspect of the vertex. The median ocellus is in the epicranial suture, somewhat ventrad of the lateral ocelli. In *Leia* it is in this suture somewhat dorsad of the bifurcation, and the other two ocelli are somewhat laterad of it. This location of the ocelli in the Diptera agrees with Comstock's idea concerning the caudal migration of the ocelli in specialized insects. In generalized insects all three ocelli may be on the front or two on the vertex while the median ocellus is on the front. The ocelli in the Hymenoptera and Hemiptera are similar in location to those of the Diptera.

*Leia* is the only form studied which has ocelli and a well-marked stem of the epicranial suture. The chitinized, secondary, Y-shaped thickenings on the ocellar triangle of *Rhyphus* (Fig. 9) and *Mycetobia* (Fig. 7) should not be confused with the epicranial suture. Three ocelli are present in all other genera of Diptera examined except *Oncodes* (Fig. 53) and *Mycetophila*, in which there are only two. The median ocellus is wanting in *Mycetophila*, while the lateral ocelli are small inconspicuous bodies, adjacent to the dorso-mesal margin of the compound eyes (not shown in the figure). The figures show such variations as occur in the various ocellar groups.

*Occiput and Postgenae*.—No sutures occur on the caudal aspect of the hypothetical head-capsule (Fig. 73) except the epicranial suture (e.s). This absence of sutures makes it impossible to locate definitely the boundaries of the occiput and the postgenae. The following interpretation is based upon a study of the occiput and postgenae of generalized insects, such as the Orthoptera. The occiput comprises all the area dorsad of an imaginary transverse line drawn thru the middle of the centrally located occipital foramen. The areas ventrad of this line and laterad of the mesal membranous areas are the postgenae. The occiput (occ) undergoes a secondary development about the margin of



the occipital foramen. The structures pertaining to this modification have been designated as the parocciput (pocc). Each postgena (po) is also secondarily differentiated along its mesal margin by a chitinized thickening which extends between the occipital foramen and the invaginations of the posterior arms of the tentorium. This thickening has been designated as the parapostgenal thickening, while the area mesad of it is the parapostgena (ppo). The two mesal projections of the parocciput on the lateral margin of the occipital foramen serve as points for the articulation of neck sclerites and mark the ventral boundary of the occiput.

The occipital foramen (o. f) is centrally situated in all but a few genera, such as *Tipula* (Fig. 95), *Limnobia* (Fig. 93), *Psorophora* (Fig. 96), and *Bibio* (Fig. 92), in which it is near the dorsal margin. The size of the occipital foramen is more or less constant thruout the order, but in *Psychoda* (Fig. 82) and *Promachus* (Fig. 84) it is comparatively much larger than in *Pipunculus* (Fig. 106) and *Exoprosopa* (Fig. 98). The shape of the occipital foramen varies somewhat, but usually it is in the form of a figure eight. The constrictions in the lateral margins are generally due to the mesal projections of the parocciput, which vary to some extent in their situation. The projections in *Exoprosopa* (Fig. 98), *Pipunculus* (Fig. 106), and *Mydas* (Fig. 99) meet on the meson and completely divide the occipital foramen into two openings. The neck sclerites (n. s) always articulate with these mesal projections and are represented in a number of the figures.

The occiput (occ) of all genera figured resembles in general the occiput of the hypothetical head, since no sutures separate the vertex, the occiput, and the postgenae. The position of the occipital foramen and the contour of the caudal surface determine the amount of variation in the occiput as well as in the postgenae. In some genera, *Empis* (Fig. 164) and *Bibiocephala* (Fig. 156), the caudal aspect is convex; while in others, *Exoprosopa* (Fig. 98) and *Pipunculus* (Fig. 106), it is decidedly concave. Suture-like markings or depressions are present near the dorsal margin of the caudal aspect in the heads of *Tabanus* (Fig. 74), *Stratiomyia* (Fig. 104), *Bibio* (Fig. 91), *Bibiocephala* (Fig. 83), *Leptis* (Fig. 103), *Psilocephala* (Fig. 100), and others. These depressions mark the place of contact of the mesal portions of the ocular sclerites with the head-capsule, and are in no way homologous with the sutures about the occiput in generalized insects.

The area about the dorsal and lateral margin of the occipital foramen, the parocciput (pocc), is more or less differentiated from the remainder of the occiput in all the species studied. In the more generalized forms, *Bibiocephala* (Fig. 83), *Trichocera* (Fig. 78), *Tipula* (Fig. 95),

Sciara (Fig. 81), and Bittacomorpha (Fig. 85), it is only a thickened edge; but in a large number of species thruout the order it is a clearly defined piece, set off from the occiput proper by a secondary suture. The indefiniteness of this piece in a large number of the generalized Diptera and the want of an homologous part in generalized insects support the view that it is only a secondary modification of the occiput.

The parocciput (poce), in most genera, occurs as a narrow piece about the dorsal and lateral margin of the occipital foramen, and its ventral ends project mesad. In the heads of the Cyclorrhapha three secondarily developed, chitinized thickenings (th) arise from the ental surface of the parocciput; two of these project dorso-laterad from the lateral portions of the parocciput, and the third is on the meson. These thickenings are also present in some of the Brachycera, such as Dolichopus (Fig. 112). Their greatest development is found in Eristalis (Fig. 113), where two dorso-lateral thickenings (th) extend to the caudal margins of the compound eyes and a third thickening, on the meson, bifurcates a short distance dorsad of the occipital foramen, the two arms connecting with the dorso-mesal angles of the compound eyes. In the genera figured, the dorso-lateral thickenings are, on the whole, better developed than the thickening on the meson. In Thelaira (Fig. 128) and Musca (Fig. 133) the dorso-lateral thickenings project dorsad to the margin of the head. The area included between them is called by several writers the epicephalon, or the occiput; and tho it is entirely different in origin from similarly situated areas in Tabanus (Fig. 74) and other genera, the same name is applied in the different cases. These names and others used by systematists have no morphological significance for they can not be homologized with the primary sclerites of a generalized insect.

The postgenae (po) of the hypothetical dipterous head have been carefully compared with those of the heads of such generalized insects as the Orthoptera. The mesal membranous area between the postgenae is homologous with the membrane of the neck and with the membrane surrounding the proximal ends of the maxillae and the labium. There are no sutures or sclerites along the mesal portions of the postgenae in such generalized insects as the Orthoptera; consequently the parapostgenae (ppo) described above can not be homologous with any primary sclerite. In Diptera the parapostgenae are undoubtedly special modifications of the postgenae.

The postgenae and the parapostgenae of a majority of the Nematocera resemble those of the hypothetical head. In Chironomus (Fig. 88) and Trichocera (Fig. 78) the parapostgenal thickenings are wanting. The invaginations for the posterior arms of the tentorium in

*Simulium* (Fig. 77) are adjacent to the occipital foramen, consequently the parapostgenae are confined to the lateral margins of the occipital foramen. In *Tabanus* also the invaginations are adjacent to the occipital foramen, and the postgenae are connected ventrad of the occipital foramen in the male and by a narrow strip in the female.

4/ The area ventrad of the occipital foramen is a continuous chitinized piece in all of the *Cyclorrhapha* and the *Orthorrhapha*. There is only one probable explanation of the origin of this area. It has been derived from the fusion of the mesal margins of the postgenae. The evidence for this interpretation is found in a number of the *Nematocera*. The mesal margins of the postgenae in *Trichocera* (Fig. 78) and *Sciara* (Fig. 81) are curved mesad and in some cases actually join, as in the female of *Bibiocephala* (Fig. 83). The peculiar elongated heads of *Limnobia* (Fig. 93), *Tipula* (Fig. 95), and *Psorophora* (Fig. 96) show a distinct depressed line on the meson along which the postgenae have joined. In a number of the genera of the *Orthorrhapha* and the *Cyclorrhapha* the ventral margin of the caudal aspect is decidedly concave. This condition may be due to a former stage in the development of the fused postgenae. In all cases where the area ventrad of the occipital foramen is chitinized, the invaginations of the posterior arms of the tentorium are somewhat adjacent to the occipital foramen and the attachments of the maxillae are removed to or beyond the ventral margin of the head. *Sciara* (Fig. 81) is a good example of an early stage in the development of the above relationship. The variations in the shape and extent of the postgenae and the parapostgenae are well illustrated by the figures.

*Tentorium*.—There is present within the head of generalized insects a definite arrangement of chitinized rods and plate-like structures which go to support the internal organs and furnish places for the attachment of muscles. These rods or plates arise from three pairs of openings on the head known as the invaginations of the anterior arms, dorsal arms, and posterior arms of the tentorium. The invaginations of the anterior arms are usually associated with the lateral margins of the clypeus, with one of the points of articulation of the mandibles, and frequently with the ventral ends of the arms of the epicranial suture. The invaginations of the dorsal arms are associated with the points of attachment of the antennae and near the dorsal portions of the arms of the epicranial suture. The invaginations of the posterior arms are associated with the occipital foramen and the points of attachment of the maxillae. The three pairs of arms unite within the head; the small dorsal arms unite with the larger anterior arms, and these, in turn, join with the posterior arms, which are confined to the caudal portion of the head.



capsule. The free ends of the posterior arms are fused and form the body of the tentorium.

The tentorium undergoes a considerable amount of variation in the different orders, but so far as observed the above associations between the invaginations and the fixed and movable parts of the head are always retained by the more generalized members of each order. This is also true for a generalized hypothetical dipterous head. The tentorium (t) of such a head (Fig. 140 and 141) is considerably modified when compared with the tentorium of a generalized insect. Two pairs of invaginations are present on the cephalic aspect of the head (Fig. 1). The dorsal, indistinct pair (i.d), just ventrad of the antennae, are homologous with the invaginations of the dorsal arms of the tentorium, while the prominent pair (i.a) of invaginations ventrad of these and located in the arms of the epicranial suture (a.e.s) and adjacent to the lateral ends of the fronto-clypeal suture are the invaginations of the anterior arms of the tentorium. One pair of invaginations (i.p) is present on the caudal aspect of the head-capsule (Fig. 73) somewhat ventrad of the ventro-lateral margins of the occipital foramen. These are the invaginations of the posterior arms of the tentorium. Each lateral half of the tentorium is Y-shaped (Fig. 141), the stem of the Y arising from the invaginations on the caudal aspect, its caudal portion being a part of the posterior arms (p.a) of the tentorium. The large ventral arm of the Y and the cephalic portion of its stem, constitute the anterior arm (a.a), and the small dorsal arm of the Y is the dorsal arm (d.a) of the tentorium. These two arms connect with their respective invaginations on the cephalic aspect. The body of the tentorium (b.t) is apparently represented by a small, rudimentary, mesal projection arising from the posterior arms near the caudal portion of the stem of the Y.

The association between the movable appendages and the invaginations of the tentorium is discussed under the respective appendages. From this point, the tentorial structures as they occur in the various genera are compared with the hypothetical type and the line of specialization noted. The forms without a ptilinum are considered first. The parts of the free tentorium, not completely fused with the head-capsule, are indicated in the figures by dotted lines.

The tentorium of *Tabanus* (Fig. 142 and 143) is generalized and closely resembles the hypothetical type; consequently it furnishes a good starting point for a discussion. Two pairs of invaginations are present on the cephalic aspect (Fig. 20); of these the invaginations for the anterior arms (i.a) are the more prominent. The dorsal arms (i.d) arise from the head-capsule just ventro-laterad of the antennae

and connect with the arms of the epicranial suture (a.e.s). The invaginations of the anterior arms are situated near the ventral ends of the arms of the epicranial suture. The invaginations on each lateral half of the head are joined together by the arms of the epicranial suture and resemble the hypothetical type. Two pairs of invaginations are also present on the cephalic aspect of *Simulium* (Fig. 2 and 3), but in this genus they are not as prominent as in *Tabanus*. They are situated on the vertex (v), adjacent to the compound eyes. In the female the arms of the epicranial suture are well defined and the invaginations are closely adjacent to them, while in the male the sutures are wanting. *Tabanus* and *Simulium* are the only forms figured which show two distinct pairs of invaginations on the cephalic aspect. All other genera have only one pair and these are of two types. They are either long and slit-like or they resemble small pits or darkened spots on the ectal surface. The long slit-like invaginations found in *Leptis* (Fig. 35), *Psilcephala* (Fig. 36), *Platypeza* (Fig. 32), *Scenopinus* (Fig. 41), *Exoprosopa* (Fig. 29), *Stratiomyia* (Fig. 27), *Mydas* (Fig. 30), *Eristalis* (Fig. 25), and other genera have a special significance which will be more fully discussed later. The small, pit-like invaginations are present in the *Nematocera* and in *Pipunculus* (Fig. 38) and *Empis* (Fig. 40). These are situated on the chitinized area of the vertex; or on the fronto-clypeus, adjacent to the arms of the epicranial suture and usually close to the compound eyes. Their position and structure indicate that they are the invaginations of the anterior arms of the tentorium. In a few of the genera of the *Orthorrhapha* and in some others, as *Lonchoptera* (Fig. 37), *Tipula* (Fig. 18), and *Aphiochaeta* (Fig. 31), no invaginations are present on the cephalic aspect of the head.

One pair of invaginations, that for the posterior arms (i.p) of the tentorium, is present on the caudal aspect of the heads of all genera examined except *Oncodes* (Fig. 105), *Olfersia* (Fig. 139), *Tipula* (Fig. 95), and perhaps a few species of other genera in which it is difficult to be sure of their presence. These invaginations in *Bibliocephala* (Fig. 83), *Trichocera* (Fig. 76), *Dixa* (Fig. 79), *Rhyphus* (Fig. 80), *Sciara* (Fig. 81), *Psychoda* (Fig. 82), *Rhabdophaga* (Fig. 86), *Chironomus* (Fig. 88), *Bittacomorpha* (Fig. 85), *Mycetophila* (Fig. 87), and *Mycetobia* (Fig. 90) are decidedly ventrad of the occipital foramen and adjacent to the proximal ends of the maxillae. They are connected with the lateral margins of the occipital foramen by means of the para-postgenal thickenings except in *Chironomus* and *Trichocera*. The above-named forms closely resemble the hypothetical type. In a few genera of the *Nematocera*, such as *Psorophora* (Fig. 96) and *Simulium* (Fig. 77), the invaginations are adjacent to the occipital foramen. This



position is characteristic of these invaginations in the Brachycera, and the figures show the details of the variations in the position of the invaginations on the posterior arms of the tentorium.

Two lines of specialization appear in the tentorium of the Diptera, one in the reduction of the dorsal arms and the other in the union of the dorsal arms with the anterior arms. The two types of invaginations described for the cephalic aspect of the head bear directly upon this problem. The most important evidence in proof of these two types of development is found in the structure of the arms.

In *Sciara* (Fig. 150), *Bibio* (Fig. 153 and 154), *Psorophora* (Fig. 159), *Trichocera* (Fig. 158), *Bibliocephala* (Fig. 155), *Dixa* (Fig. 163), and others, two long narrow rods extend on each side between the invaginations on the caudal aspect and the invaginations on the cephalic aspect. These rods are composed of the posterior arms (p. a) and the anterior arms (a. a) of the tentorium. The dorsal arms are completely reduced in these forms. Other genera show completely developed dorsal arms or rudiments of the same. The dorsal arms (d. a) are distinct and free in *Pipunculus* (Fig. 151). They arise from the anterior arms and project cephalad to the cephalic aspect of the head, where they connect with small but distinct ental projections adjacent to the antennae. The cephalic ends of the dorsal arms are very delicate and easily broken in dissecting. There are no invaginations on the ectal surface. In *Chironomus* (Fig. 152) the tentorial arms are swollen near the middle of their length, and the distinct humps on the dorsal side are interpreted as rudiments of the dorsal arms. *Promachus* (Fig. 147) has two long, free, finger-like projections, arising from the ocular sclerite near the antennae, which project toward the tentorium proper. These projections are apparently dorsal arms of the tentorium, or derivatives of the same that have retained their connection with the ocular sclerite near the mesal margin of the compound eye but have lost their connection with the tentorium proper. A similar relationship exists between the dorsal arms and the ocular sclerite in *Tabanus* (Fig. 22). If the above structures in *Promachus* are dorsal arms, then the anterior arms are large (Fig. 148) and the slit-like invaginations on the cephalic aspect are only the invaginations of the anterior arms of the tentorium.

The tentoria of the Nematocera above described are in the ventral half of the head-cavity and their situation is dependent upon the position of the invaginations. Usually the invaginations of the anterior arms are ventrad of the invaginations of the posterior arms; but *Bibliocephala* (Fig. 155) is an exception to this rule if the tentorium in this genus is composed of only the anterior and posterior arms—and there

is no evidence to the contrary. In some genera, as in *Lonchoptera* (Fig. 177), *Rhabdophaga* (Fig. 170), and *Empis* (Fig. 164), the tentoria are not free rods extending thru the head cavity, but are completely united with the ventral margin of the head, or nearly so. The tentorium of *Aphiochaeta* (Fig. 174) is reduced to two small ental projections adjacent to the occipital foramen, while in *Tipula* (Fig. 178) the tentorium is apparently wanting.

In a majority of the *Brachycera* the tentorial arms are specialized by fusion, and *Tabanus* (Fig. 143) illustrates an early stage in this development. The principal difference between the tentorium of *Tabanus* and the hypothetical type is the presence of a thin chitinized plate in the V-shaped opening between the anterior and dorsal arms. *Simulium* (Fig. 144), of the *Nematocera*, has a similar plate, and these two genera clearly demonstrate the first stage in the fusion of these two arms. The cephalic end of the tentorium in *Mydas* (Fig. 146), *Leptis* (Fig. 145), *Scenopinus* (Fig. 149), and *Exoprosopa* (Fig. 162) is a broad uniformly chitinized triangular area. This condition is accounted for on the basis of the union of the anterior and dorsal arms. The invaginations on the cephalic aspect of these forms agree in all respects with this interpretation. In *Tabanus* (Fig. 20) the invaginations on each side are joined together by the epicranial suture, while in the above forms the invaginations are slit-like and occupy the greater part of the arms of the epicranial suture. The slit-like invaginations are easily explained if the anterior and dorsal arms are considered as united.

The posterior arms of the tentoria of the *Nematocera* and the *Brachycera* vary in shape, size, and location. The anterior and posterior arms are united within the head and no sharp line can be drawn between them. The body of the tentorium (b. t) is represented by small projections on the mesal surface of the posterior arms of most genera.

Many interesting features occur in the modifications of the tentoria of this group. In *Dolichopus* (Fig. 43 and 168) it appears to be fused with the dorsal margin of the slit-like openings on each side between the mesal margin of the compound eye and the fronto-clypeus. The tentorium of *Mydas* (Fig. 146) is large and tubular, and it is possible to push a good-sized needle thru the opening on the cephalic aspect to the opening of the posterior arms on the caudal aspect.

The tentoria of the genera possessing a ptilinum differ principally from the foregoing in the degree of fusion with the head-capsule. In most genera of this group the tentorium is completely united with the head, but in a number of the *Acalyptratae* the tentorial arms arise as free rods from the invaginations on the caudal aspect and project to the latero-ventral margins of the head-capsule, with which they unite

and continue cephalad as thickenings adjacent to the ventral margin of the head, as in *Sapromyza* (Fig. 171), *Loxocera* (Fig. 169), *Euaresta* (Fig. 175), *Calobata* (Fig. 183), *Chrysomya* (Fig. 181), *Drosophila* (Fig. 172), *Chyromyia* (Fig. 179), *Heteroneura* (Fig. 176), and *Tetanocera* (Fig. 180). In those forms where the tentorium is completely fused with the head, as in *Sepsis* (Fig. 184), *Chloropisca* (Fig. 189), *Coelopa* (Fig. 182), and *Borborus* (Fig. 188), it is a continuous thickening from the latero-ventral angle of the occipital foramen to the cephalo-ventral aspect of the head-capsule. The tentorium between the invaginations for the posterior arms and the ventro-lateral margins of the head-capsule is apparently wanting in *Musca* (Fig. 194), *Thelaira* (Fig. 196), *Archytas* (Fig. 197), and some other genera; in one or two cases it is possible to trace a faint mark which would indicate the line of connection. The tentoria of some of the genera of the Acalyptratae and the Calyptratae show an unusual development of the tentorial thickenings (t. th) in that they extend about the entire caudal part of the ventral margin of the head. In some cases these tentorial thickenings reach the occipital foramen, as in *Calobata* (Fig. 114), *Scatophaga* (Fig. 135), *Heteroneura* (Fig. 126), *Lispa* (Fig. 116), and *Myiospila* (Fig. 120), while in *Musca* (Fig. 133), *Coelopa* (Fig. 121), *Hydrotaea* (Fig. 127), and other genera, there is no such connection.

The invaginations of the posterior arms of the tentorium of the Acalyptratae and the Calyptratae are situated laterad or latero-ventrad of, and adjacent to, the occipital foramen. In many of the species figured the invaginations are merely long, heavily chitinized furrows extending latero-ventrad from the occipital foramen, and very often it is difficult to locate them definitely.

Two mesal projections arise from the proximal portions of the posterior arms in a majority of the Cyclorrhapha. In some species these structures are well developed, and their mesal ends apparently join on the meson, cephalad of the occipital foramen. These structures are similar to those described for the Brachycera and are rudiments of the body of the tentorium.

No invaginations of the tentorium occur on the cephalic aspect in any of the forms which possess a ptilinum. On account of the decided specialization of this aspect, it is very difficult to know just what has happened. The tentorium is represented by thickenings which extend from the ventral to the cephalic aspect of the head. The extent of these thickenings varies; in some genera they continue to the antennal fossae, while in others they are practically wanting.



## MOVABLE PARTS OF THE HEAD

In arrangement and structure the movable parts of the head of the generalized Diptera are homologous with the movable appendages of other generalized insects. In the Cyclorrhapha the parts retain their relative position, but structurally they undergo striking modifications and in some cases almost complete reduction.

To make clear the use of a number of terms found in the following discussions, the mouth-parts as a whole will be considered at this point. The appendages of the mouth of the generalized Diptera are free, independent structures, with their proximal ends adjacent to the head-capsule. The cardines and stipites of the maxillae are exceptions to the above statement, in that they are embedded in the mesal membranous area of the caudal aspect of the head. The mouth-parts, the labrum-epipharynx, and the hypopharynx constitute in the Calyptratae a single complex mouth-appendage designated as the proboscis. The chitinized parts of the proboscis are far removed from the head-capsule, but in this projection of the parts, the proximal ends of the chitinized appendages are joined together and have the same relationship with each other as in generalized insects.

The term proboscis is most applicable among the Cyclorrhapha to those whose mouth-parts resemble those of Musca. The proboscis is naturally divided into three areas by the two bends which it makes as it is withdrawn into the oral cavity. The parts of the proboscis have been given varied and confusing names. Hewitt divides it into two general areas—the rostrum and the proboscis proper. He says: "The proboscis consists of two parts, a proximal membranous conical portion, the rostrum, and a distal half, the proboscis proper, which bears the oral lobes. The term haustellum is also used for this distal half (minus the oral lobes) and as a name it is probably more convenient, as the term proboscis is used for the whole structure,—rostrum, haustellum and oral lobes".

The terms rostrum and haustellum have been used in various ways by numerous workers in different orders; consequently the parts which they designate are by no means homologous. A more comprehensive set of terms based upon the word proboscis has been used by a few workers, who divide the proboscis into basiproboscis, mediproboscis, and

distiproboscis. These terms have here been adopted. The basiproboscis (bpr) is equivalent to the rostrum, and may be defined as the membranous, cone-shaped area between the ventral margin of the head-capsule and the proximal end of the theca. The tormae, labrum-epipharynx, hypopharynx, and maxillae are parts of the basiproboscis. The mediproboscis (mpr) is the median section of the proboscis and includes the theca and the chitinized cephalic groove of the labium. It is equivalent to the haustellum of most authors. The distiproboscis (dpr), the enlarged dilated lobes at the distal end of the proboscis, is composed of the paraglossae, with their pseudotracheal areas, and the glossae. The distiproboscis is equivalent to the oral lobes, or labellae. The movable appendages of the head are discussed in the following order: antennae, mandibles, maxillae, and labium.

*Antennae.*—The antenna of a generalized hypothetical dipterous head (Fig. 199h) is many-segmented and of a filiform type. All the segments are similar excepting the two large proximal ones known as the scape (sc) and the pedicel (pd). The scape articulates with the chitinized antennal sclerite (a.s) which bounds the periphery of the antennal fossa (a.f) that is situated on the vertex dorsad of the arms of the epicranial suture. The antennae of the hypothetical type resemble the antennae of many generalized insects.

The antennae of a majority of the Nematocera resemble the hypothetical type, and on the whole resemble each other. The variations in shape and size can be seen in the figures. Secondary sexual variation occurs in a few of the Nematocera, in which the antennae of the male, illustrated by *Chironomus* (Fig. 207) and *Psorophora* (Fig. 211), bear long flexible setae while those of the female are almost bare.

The antennae of the Brachycera show a wide range of development, but in a majority of the genera figured the main line of specialization is toward the type found in *Lonchoptera* (Fig. 223) and *Dolichopus* (Fig. 226). One of the striking exceptions to this general line of development occurs in the geniculate type found in *Stratiomyia* (Fig. 213). The antennae of the Brachycera have, as a rule, fewer segments than the Nematocera. The scape and pedicel undergo only a slight change, in this group, but the flagellum (fl) is greatly modified. The proximal segment of the flagellum, or the third segment of the antenna, is enlarged, while the remaining segments are so reduced in size as to resemble the lash of a whip. The lash-like portion of the antenna is called the arista (ar). The following genera suggest the various stages thru which the antennae have passed in attaining the muscid type of development. In *Tabanus* (Fig. 214), *Empis* (Fig. 215), *Exoprosopa* (Fig. 216), *Promachus* (Fig. 217), and *Leptis* (Fig. 218) the flagellum

is styletate, and the third segment is large and conical, with one or more segments at its distal end. The antennae of *Platypeza* (Fig. 222), *Lonchoptera* (Fig. 223), *Aphiochaeta* (Fig. 224), *Oeciothea* (Fig. 227), and *Dolichopus* (Fig. 226) show an advanced stage of development in which the third segment is large and round and the remaining segments are lash-like and situated toward one side of the third segment. All but a few of the antennae of the *Cyclorrhapha* have apparently developed from a type similar to the last-mentioned genera. The principal differences between the antennae of this group are in the length and breadth of the third segment and in the modification of the arista. The antennae of *Olfersia* (Fig. 249) are of a reduced muscid type, and are inserted in deep cavities on the cephalic aspect of the head; the scape and pedicel are greatly reduced, and the arista is merely a small projection on the lateral aspect of the large segment.

Antennal sclerites (a. s.) are present only in *Chironomus* (Fig. 12 and 206) and *Psorophora* (Fig. 10 and 26). In these genera it is a distinct chitinized ring about the proximal end of the scape. The extent and place of the membrane with which the antennae are connected vary considerably. In *Trichocera* (Fig. 16), *Chironomus* (Fig. 12), *Psorophora* (Fig. 26), *Mycetobia* (Fig. 7), and some other genera it is very extensive.

A general survey of the antennae of the *Diptera* shows that in the *Nematocera* they are generalized and on the whole resemble each other. The specialized antennae of the *Cyclorrhapha* in all but a very few genera are of a muscid type, and also quite similar in form. The antennae of the *Brachycera* present a few specialized types, but the majority of them show intermediate stages between the forms found in the *Nematocera* and those of the *Cyclorrhapha*.

*Mandibles*.—Only a few of the generalized *Diptera* possess mandibles. They are present in the females of *Simulium* (Fig. 2 and 250), *Tabanus* (Fig. 255 and 317), *Psorophora* (Fig. 159 and 251), *Culicoides* (Fig. 253), *Dixa* (Fig. 254), and *Bibiocephala* (Fig. 155 and 256), but wanting in the males of all the species examined except *Simulium* (Fig. 3 and 252). The males of *Simulium johannseni* and *S. jenningsi* have distinct mandibles. No other males of *Simulium* were examined. So far as known this is the first record of a male dipteran possessing true mandibles.

The hypothetical mandibles (Fig. 256h) of a dipteran are long, thin, sword-shaped structures fitted for piercing. They thus resemble the mandibles (md) of *Tabanus* (Fig. 255) and *Culicoides* (Fig. 253). They are situated between the clypeus, labrum-epipharynx, and maxillae, and are closely associated with the invaginations of the anterior



arms of the tentorium. Structurally the hypothetical mandibles do not resemble the biting mandibles of the Orthoptera, but their situation and their association with the invaginations of the anterior arms of the tentorium are the same, which is far more important in determining their homology than any particular form they may assume.

The mandibles vary in their structure. In *Psorophora* (Fig. 251) they are long and needle-like, while in *Tabanus*, *Culicoides*, and the male of *Simulium* (Fig. 252) they are sword-shaped, and in *Dixa* (Fig. 254) spindle-like. The mandibles in the females of all species of *Simulium* (Fig. 250) examined are a trifle longer than those in the males (Fig. 252) and much broader at their distal ends. The greatest specialization in structure and point of attachment with the head occurs in the long, thin, saw-like mandibles of *Bibiocephala* (Fig. 256) and *Blepharocera*. In these forms they are longer than the labium, blunt at the end, and toothed along the mesal margin, fitting against a similar edge on the lateral margin of the hypopharynx.

All mandibles (md) of the Diptera are connected with the head-capsule cephalad of the maxillae (mx) and caudad of the labrum-epipharynx (l.ep) and the fronto-clypeus (fr.c). In this respect they resemble the hypothetical type. In *Psorophora*, *Dixa*, *Simulium*, and *Tabanus* they are associated with the invaginations of the anterior arms of the tentorium. The proximal ends of the mandibles of *Psorophora* (Fig. 159) are bent cephalad, and articulate with the head-capsule at the distal ends of the crescent-shaped tentorial thickenings (t.th) which arise from the margins of the invaginations of the anterior arms of the tentorium. In *Dixa* (Fig. 254) the mandibles connect with the head-capsule at the ventro-caudal angles of the clypeus. An indistinct thickening extends dorsad from the point of articulation of each of the mandibles toward the invaginations of the anterior arms of the tentorium. The mandibles of *Simulium* (Fig. 250 and 252) and *Tabanus* (Fig. 317) connect with the head-capsule directly ventrad of the invaginations of the anterior arms of the tentorium, but no direct connection occurs between them. In the female of *Simulium* the mandibles articulate with a hook-shaped projection of the vertex. The mandibles of *Tabanus* (Fig. 255) are bifurcate at their proximal end and the lateral bifurcation articulates with the head. The location of the mandibles of *Bibiocephala* (Fig. 155) and *Blepharocera* is generalized with respect to their position between the maxillae and the fronto-clypeus, but their point of attachment with the head-capsule is decidedly specialized. They unite with chitinized pillars (Fig. 83) on the caudal aspect ventro-laterad of the invaginations of the posterior arms of the tentorium. The proximal portion of each mandible is a long chitinized strip

embedded in the membrane. These strips extend cephalad from their caudal connection to the cephalic margin of the membrane about the mouth-parts. At this point, where distinct tendons are attached, they turn abruptly ventrad and become free appendages. All connection between the mandibles and the invaginations of the anterior arms of the tentorium is lost. The relationship between the tentorium and the mandibles has not been observed in *Culicoides* for the lack of material. No other families of the *Diptera* outside of those to which the above-named genera belong, so far as observed, possess true mandibles or rudiments of the same. When mandibles are present, they are always of considerable size and probably functional.

A number of investigators have described mandibles for many species not included in the above families. Langhoffer (1901) describes mandibles for the *Dolichopodidae* which are shown in this paper to be modifications of the epipharynx (Fig. 524 and 528). The apodemes of the muscids (Fig. 304, 308, and others) have been called mandibular tendons by MacCloskie and others. This is incorrect as shown by the figures and in the discussion of the maxillae. A number of workers (e. g., Wesché, 1909) believe that the mandibles have united with the labium and exist as chitinized strips on the cephalic aspect of the labium or as thickenings on the meson of the theca. Neither of these interpretations can be accepted when one takes into consideration the relative position of these so-called mandibles and the manner of development of the proboscis of the *Calyptratae*. The chitinized thickenings on the cephalic aspect of the labium are located caudad of the maxillae and the hypopharynx. This does not agree with the position of the mandibles of other insects. Furthermore, these thickenings are present in *Tabanus* where true mandibles occur. The chitinized thickenings on the meson of the theca in some of the *Diptera* can not be considered as rudiments of mandibles for many reasons. The most conclusive objection to this interpretation lies in the fact that these thickenings are very prominent in *Simulium* which has distinct mandibles in both sexes.

When interpreting mouth-appendages, it is always necessary to take into consideration the generalized relationship between the mouth-parts and their association with the invaginations of the tentorium. It is also very desirable to observe a large series of forms before attempting to homologize the parts. The above interpretations were apparently not made from either of these vantage-points.

*Maxillae*.—All *Diptera* having functional mouth-parts have maxillae. They are, however, greatly reduced and modified in some genera, and at first glance bear little or no relation to the structure or location



of the maxillae of generalized Diptera or other insects. Numerous intermediate stages of maxillary development are present in the various species; consequently it is possible, and in fact comparatively easy, to trace thruout the order the main line of specialization and several side lines.

The hypothetical maxillae of the Diptera (Fig. 257) resemble the maxillae of a generalized insect in their homologous sclerites, their position between the mandibles and the labium, and their close association with the invaginations of the posterior arms of the tentorium. Structurally they are composed of small triangular cardines (ca), long stipites (st), five-segmented palpi (mx.pl), needle-like galeae (g), and short laciniae (la). The cardines and stipites differ from those of generalized insects in that they are embedded in the mesal membranous area ventrad of the occipital foramen. The palpi, galeae, and laciniae are free appendages. The proximal ends of the cardines are adjacent to the invaginations of the posterior arms of the tentorium. The structure and position of the various parts of the hypothetical type have been traced thruout the order. The species in which the ptilinum is wanting are considered first.

The cardines (ca) are small distinct triangular sclerites in *Trichocera* (Fig. 260), *Rhyphus* (Fig. 261), *Dixa* (Fig. 262), and the female of *Tabanus* (Fig. 259). In these genera they are adjacent to the invaginations of the posterior arms of the tentorium. The cardines of *Simulium* (Fig. 258), in both males and females, differ from those of the above genera in that they are large and occupy nearly all of the membranous area between the postgenae dorsad of the stipites. Their margins are also somewhat indistinct. No other forms figured have distinct sclerites that are homologous with the cardines of the hypothetical type. The maxillae of *Rhabdophaga* (Fig. 268), *Bibiocephala* (Fig. 269), and *Chironomus* (Fig. 270) connect with the invaginations of the posterior arms by means of narrow chitinized processes which arise from the stipites proper. Undoubtedly these pieces are reduced cardines which have lost the suture that separates them from the stipites. The presence of this suture is suggested by the suture-like depression in the male of *Bibiocephala* (Fig. 76). Excepting *Promachus* (Fig. 276) and the above forms, the cardo is wanting in all the maxillae figured. The maxillae of *Psychoda* (Fig. 263) and *Sciara* (Fig. 267) closely resemble some of the above maxillae, but the cardines as chitinized pieces are apparently wanting. There is a distinct membranous area between the proximal ends of the stipites and the invaginations of the posterior arms of the tentorium. From forms such as these it is concluded that the cardines have been lost as chitinized areas. No other interpretation seems possible with the evidence at hand.

The stipites (st) are of various shapes and sizes as can be seen in the figures. In *Rhabdophaga* (Fig. 268), *Bibiocephala* (Fig. 269), *Chironomus* (Fig. 270), and possibly *Mycetobia* (Fig. 90), they have united to form a chitinized strip or plate in the membranous area dorsad of the labium. This piece should not be confused with the submentum of the labium. In all species in which the postgenae have not united ventrad of the occipital foramen, the proximal ends of the stipites are near the invaginations of the posterior arms of the tentorium. In all species where the postgenae form a continuous plate, the stipites are reduced in size and situated at or beyond the ventral margin of the head, as in *Mydas* (Fig. 319) and *Eristalis* (Fig. 328). In other words, the usual association between the maxillae and the invaginations of the posterior arms has been lost. *Psilocephala* (Fig. 281) and *Psorophora* (Fig. 96) are exceptions to the last statement. In *Psilocephala* chitinized thickenings (ch.th) are present on the ental surface of the postgenae ventrad of the occipital foramen, and these are undoubtedly rudiments of the stipites. The stipites of *Psorophora* (Fig. 266 and 96) are long, free rod-like structures located entad of the postgenae. They extend between the occipital foramen and the ventral margin of the head. The stipites of *Geranomyia* (Fig. 382) and *Limnobia* (Fig. 386) are also entad of the postgenae. In these genera their proximal ends are united and they have no connection with the head-capsule. The stipites of *Tipula* (Fig. 277) resemble those of *Geranomyia* and *Limnobia*, but there is greater reduction in size, and they are completely united along their mesal margins, thus forming a single median piece.

The maxillae of *Promachus* (Fig. 84) differ from those of all other genera in that the stipites and the cardines are united on the meson and continuous with the postgenae near the occipital foramen. Narrow membranous areas separate the maxillae from the postgenae near the ventral margin of the head. This unique modification of the maxillae agrees with the striking modifications in the other mouth-parts.

The figures show the variations in other genera belonging to this group. In general it can be said that the stipites have been modified by reduction and by removal to the ventral margin of the head and in some cases are even located on the basiproboscis.

The maxillary palpi (mx. pl) of the Nematocera figured have from two segments—*Geranomyia* (Fig. 382) and the female of *Psorophora* (Fig. 266)—to five segments. The usual number is four or five. In the Brachycera only one articulating segment is present. This segment in *Tabanus* (Fig. 259) connects with an elongated portion of the stipes which is called the palpifer by some. In this study the palpifer is considered as wanting, since no palpus of the Diptera possesses over

five segments and furthermore no piece is present at the base of any generalized palpus which can be homologized with the palpifer of generalized insects. The greatest reduction in the palpus of the Nematocera occurs in *Geranomyia* (Fig. 382), while in the Brachycera the palpus of *Mydas* (Fig. 271) is a mere lobe.

A small finger-like structure arises from the ventro-mesal margin of each stipes and projects mesad to the caudal aspect of the hypopharynx in *Tabanus* (Fig. 259) and *Simulium* (Fig. 258). These pieces are apparently homologous with the laciniae (la) of generalized insects. The distal ends of these projections articulate against the caudal aspect of the hypopharynx (Fig. 496 and 497), and in this respect they differ from the laciniae of generalized insects. These pieces in *Tabanus* have been described as laciniae by Patton and Cragg (1913).

A distinct lobe is present mesad of the palpus in the majority of the Diptera that do not have a ptilinum. This structure is unquestionably the galea (g), for in specialized insects which possess a distinct galea the lacinia is generally reduced in size and in some cases wanting. This tendency of development prevails in the Diptera. If the above pieces in *Tabanus* and *Simulium* which are described as laciniae are truly such, there can be no question regarding this interpretation of the lobe adjacent to the palpus. The galeae vary considerably in size and shape. They are long and needle-like in *Tabanus* (Fig. 259), in the female of *Psorophora* (Fig. 266), and in *Empis* (Fig. 274), *Exoprosopa* (Fig. 285), and *Eulonchus* (Fig. 284a); while in *Trichocera* (Fig. 260), *Dixa* (Fig. 262), *Sciara* (Fig. 267), *Bittacomorpha*, *Chironomus* (Fig. 270), *Lonchoptera* (Fig. 280), *Scenopinus* (Fig. 282), and the male of *Psorophora* (Fig. 266) they are greatly reduced. In *Bibio* (Fig. 264) and *Geranomyia* (Fig. 382) they are mere rudiments. They are wanting in *Rhabdophaga* (Fig. 268), *Tipula* (Fig. 277), *Helobia* (Fig. 385), *Aphiochaeta* (Fig. 278), *Pipunculus* (Fig. 279), *Platypeza* (Fig. 272), and *Dolichopus* (Fig. 284).

The development of the maxillae of the genera possessing a ptilinum will now be considered. No cardines or laciniae are present in this group. The maxillary palpi are one-segmented and are present in all forms except *Conops* (Fig. 305). The palpi interpreted here as maxillary palpi have been called labial palpi by some (e. g., Wesché, 1909). The stipites and galeae are present in all the species studied, and they undergo decided morphological changes. All connection or association between the maxillae and the invaginations of the posterior arms of the tentorium has been lost. This loss is even more pronounced than in the Brachycera, since in all but a few species figured the maxillae are far removed from the head and situated near the distal end of the



well-developed basiproboscis. This migration of the maxillae in the *Cyclorrhapha* has not altered their generalized position between the labrum-epipharynx and the labium.

The stipites of genera having a ptilinum show all stages of ingrowth from a turned-in free edge or end (st-e), to forms in which it is entirely entad of the membrane of the basiproboscis, as in *Musca*. *Eristalis* (Fig. 286), *Eulonchus* (Fig. 284a), and *Exoprosopa* (Fig. 285) are the only forms without a ptilinum which show an ental growth of the stipites. These genera make a good starting point for explaining the characteristic development found in the *Acalyptratae* and the *Calyptratae*. The following scheme of lines and dots has been adopted on the drawings in order to show the degree of ingrowth of the stipes. A continuous solid line on the stipes indicates a definite ectal boundary which connects with the membrane of the basiproboscis. A broken line indicates an ental edge or end which is free of the membrane between it and the observer. The membrane is represented by stippling. For convenience of description and homology the following division of the stipes has been made: st represents the ectal portion of the stipes and st-e the ental portion; and st is further divided into st-1' and st-2 as seen in *Coelopa* (Fig. 288).

In *Exoprosopa* (Fig. 285) and *Eulonchus* (Fig. 284a) the proximal end of the stipes is free and entad of the membrane, while the cephalic edge and the dorsal end are entad in *Eristalis* (Fig. 286). From a form similar to *Eristalis* it is possible to develop a stipes which would resemble that of *Sepsis* (Fig. 287), *Coelopa* (Fig. 288), and *Calobata* (Fig. 296). In *Sepsis* the palpus is greatly reduced, but it connects with an ectal portion of the stipes (st) which in turn gives rise to the free ental portion (st-e). The free ental part extends ventrad and is continuous with the galea, which emerges from the membrane near the base of the labrum as a free appendage. The stipes of *Coelopa* (Fig. 288), *Sapromyza* (Fig. 289), and *Sphyracephala* (Fig. 293) is similar to that of *Sepsis*, but in these forms the palpus arises from the cephalic margin of the basiproboscis. The palpus is connected with the stipes proper by means of a long chitinized strip (st-1) which is usually covered with setae. This ectal portion of the stipes (st-1) is present in all but a few genera, such as *Chloropisca* (Fig. 306), *Heteroneura* (Fig. 298), *Chyromyza* (Fig. 299), *Loxocera* (Fig. 300), and *Euaresta* (Fig. 292). In a number of forms, particularly in the *Calyptratae*, a small chitinized area is present ventrad of the palpus. This is regarded as a secondary chitinization. The ectal portion of the stipes (st-2) is present in a majority of the *Acalyptratae* and in one or two of the *Calyptratae*.

The ental portion of the stipes (st-e) is always present in the members of this group. In *Desmometopa* (Fig. 303), *Chloropisca* (Fig.



306), *Conops* (Fig. 305), and the *Calyptratae* it has no connection with the ectal portion of the stipes (st-2) or the membrane, and by many writers is commonly called the apodeme. The free so-called apodeme is unquestionably derived from the ental ingrowth of the stipes, as illustrated by the modifications found in the following genera: *Coelopa* (Fig. 288), *Sapromyza* (Fig. 289), *Tetanocera* (Fig. 297), *Archytas* (Fig. 309), *Musca* (Fig. 304), and others.

The development of the galea (g) may be traced thruout the *Cyclorrhapha* in a manner similar to that of the stipes. In *Eristalis* (Fig. 286) the galea is a long free appendage arising from the ventral end of the stipes near the proximal end of the labrum-epipharynx. Its length and size are greatly reduced in *Sepsis* (Fig. 287), but its position is identical with that of *Eristalis*. Thruout the majority of the *Acalyptratae* the position of the galea resembles that of *Sepsis*. Its size and form undergo some change, as can be seen in the figures. In the *Calyptratae* and some of the *Acalyptratae* the galea articulates with the proximal end of the labrum and is more or less firmly connected with the same. The ectal exposure of the galea is very small in these forms. The large galea of the *Acalyptratae* has been considered as the maxillary palpus by Wesché (1902). This interpretation is highly improbable.

*Labium*.—The labium is the most specialized and characteristic appendage of the mouth of *Diptera*. Its structural modifications are very striking among the specialized genera, such as the *Cyclorrhapha*. These modifications are largely due to the reduction of the parts and the excessive development of membranous areas, and they agree with similar types of modification in other head- and mouth-parts.

To explain the unique development of the labium of *Diptera*, it has been necessary to make a critical study of the generalized condition of this appendage as it occurs in the *Nematocera* and to compare it carefully with the labia of more generalized insects. As is well known, the labium of a generalized insect is the posterior, independent, flap-like mouth-part, made up of a submentum, mentum, and ligula. The ligula is further divided into palpigers, palpi, paraglossae, and glossae. The labium of a generalized dipteran resembles that of a generalized insect in its caudal position and in its independent condition, but it is very different in structure. It is more or less enlarged and not flat and flap-like, and the palpi and palpigers are always wanting, so far as observed. Since the position of the palpi and the palpigers is very useful in orienting the sclerites of the labium of generalized insects, their absence in *Diptera* makes it exceedingly difficult to homologize correctly and locate the submentum, mentum, and the parts of the ligula. The membranous condition of the labium also adds to this difficulty.

In order to get some light on this problem, a study was made of the labium, particularly the submentum and mentum, of a number of generalized insects of the more common orders. The literature of this subject was examined, but no satisfactory results were obtained from this source. After a careful study of a number of labia, the following general characteristics which bear upon the labium of Diptera, were noted. The submentum is the large proximal segment, while the mentum is usually small and in some cases very thinly chitinized and almost obsolete. The sutures separating the mentum from the submentum and the ligula are only represented by small remnants in *Melanoplus*. The ligula, so far as observed, comprises the movable parts of the labium, while the mentum and submentum are more or less firmly united with the head-capsule. The proximal part of the ligula is usually well developed and gives rise to the palpigers, palpi, paraglossae, and glossae. The glossae are located between the paraglossae, and in a number of forms a distinct depression or thickening extends proximad between the glossae and the proximal margin of the ligula.

With these observations as a basis for comparison, the labium of such generalized Diptera as *Chironomus* (Fig. 371), *Simulium* (Fig. 366), *Trichocera* (Fig. 365), *Dixa* (Fig. 375), and others may be interpreted as follows. The mesal membranous area of the caudal aspect of the head, which is bounded by the postgenae (po), the occipital foramen (o.f), and the proximal chitinized piece of the labium (the), is made up of the submentum, mentum (su.me), and the cardines (ca) and stipites (st) of the maxillae (mx). Since this area is largely membranous, it is impossible to determine the boundaries of these sclerites. The areas laterad of the cardines and the stipites apparently belong to the maxillae, while the area mesad of these parts is made up of the submentum and mentum (su.me). The important feature concerning this mesal membranous area is the fact that the maxillae and the labium both play a part in its formation. This undoubtedly indicates that the submentum and mentum, of a more or less fixed nature in generalized insects, have been more extensively fixed in the Diptera, and that the submentum and mentum are included in the membrane developed from the stipites and cardines. Such an interpretation is altogether possible, since the proximal portions of the maxillae are adjacent to the submentum and mentum in generalized insects.

The ligula (lg) of the generalized Diptera agrees with the ligula of generalized insects in that it is the movable part of the labium. Structurally it is composed of a well-developed proximal area which gives rise to two large bulb-like paraglossae (pgl) and to two small

membranous glossae (gl) which are located between the paraglossae. The palpigers and labial palpi are wanting, but if in the future some form is discovered which shows these structures, they will undoubtedly be found on the area here described as the ligula. The proximal portion of the ligula has a decided furrow or thickening on its caudal aspect along the meson. This thickening is characteristic of a number of Diptera and resembles the proximal portion of the ligula of a number of generalized insects. This mesal thickening marks the line of fusion of the two parts of the labium during embryonic development.

The above interpretation of the labium is on the whole very satisfactory for the numerous modified types found in the various families of the Diptera, and with this interpretation it is possible to formulate a hypothetical labium. This has been done in this study; but there have been added to this labium the early stages of development of the more important secondary structures which are characteristic of the labia of Diptera. It will therefore be advisable to call such a hypothetical labium a typical labium in order to distinguish it from the true hypothetical type of other parts of this study.

A typical labium of the Diptera (Fig. 1, 73, 140, 362, and 363) is made up of a submentum, mentum, and ligula. The submentum and mentum (su.me) are firmly united with the head and constitute the greater portion of the mesal membranous area of the caudal aspect of the head. The ligula (lg) is the large swollen and movable portion of the labium and consists of the mediproboscis (mpr) and the distiproboscis (dpr). The mediproboscis has a chitinized area on its caudal aspect which is commonly called the theca (the). The distiproboscis is composed of two large membranous bulb-like paraglossae (pgl) and two small membranous glossae (gl) which are located between the proximal parts of the paraglossae. The important and characteristic features of a typical labium are the chitinized pieces on the caudal and lateral aspects of the paraglossae and the trachea-like structures on the mesal aspects. The details of the various parts will be more fully discussed as each part is considered and its modification traced thruout the order.

The submentum and mentum (su.me) are present as a membranous area in a majority of the Nematocera and in the females of *Tabanus* (Fig. 74). This area undergoes considerable modification, as was seen in the discussion of the maxillae and postgenae, and is illustrated by the figures. *Rhyphus* (Fig. 80 and 374) is apparently the only genus which has within this area a chitinization which can not be considered as a modification of the maxillae or of the postgenae. This piece is a more or less distinctly chitinized, inverted-flask-shaped area between the maxillae. If this is a primary chitinization, it is probably a rem-



nant of the submentum. A similarly situated area found in *Mycetobia* has been homologized by some writers with that of *Rhyphus*. This interpretation is undoubtedly incorrect, since this area in *Mycetobia* (Fig. 90) gives rise to chitinized projections at its ventro-lateral angles and these in turn connect with the maxillary palpi and the galeae. Furthermore, the relationship which this piece bears to the proximal end of the theca (the) would tend to disprove such an interpretation. This piece in *Mycetobia* is undoubtedly a specialization of the maxillae similar to the modifications found in *Bibiocephala* (Fig. 83) and *Rhabdophaga* (Fig. 86). In all genera where the postgenae have grown together on the meson the submentum and mentum have been eliminated, unless one regards the area between the ventral margin of the head and the theca as derived from these areas. This area, as already described for the *Cyclorrhapha*, is very extensive and forms the caudal portion of the basiproboscis (bpr).

The proximal portion of the ligula or mediproboscis (mpr) of the typical labium is largely membranous, but it has on its caudal aspect a distinctly chitinized area, the theca (the), which has a distinct furrow on its meson. The shape, size, and degree of chitinization of the theca vary greatly, as can be seen in *Bibio* (Fig. 364), *Trichocera* (Fig. 365), *Rhyphus* (Fig. 374), *Promachus* (Fig. 376), *Tabanus* (Fig. 391), *Chyromya* (Fig. 411), *Conops* (Fig. 420), *Rhamphomyia* (Fig. 424), and *Musca* (Fig. 466). There is a distinct furrow or thickening on the meson of the majority of the *Nematocera* and the *Brachycera*, and remnants of these thickenings occur also among the *Cyclorrhapha*. In some of the *Diptera* the structural condition of the meson has a marked influence on the shape of the dorsal and ventral margins of the theca. The cephalic aspect of the proximal portion of the ligula of a typical labium is concave and membranous and connects with the proximal part of the lance-like portion of the hypopharynx. In the *Nematocera* the cephalic aspect resembles the typical labium, and in the *Brachycera* and in a majority of the *Cyclorrhapha* it has a distinctly chitinized groove. This is well illustrated by *Tabanus* (Fig. 392), *Eristalis* (Fig. 441), and a majority of the *Calypttratae*. The degree of chitinization varies considerably, and in some forms heavy, chitinized, cord-like pieces extend along the sides of the groove from the glossae to the proximal end of the labium.

The distiproboscis of the typical labium is composed of two large independent, highly membranous, bulb-like paraglossae (pgl), usually called oral lobes or labellae, and two small membranous glossae (gl). Each paraglossa has on its lateral and caudal aspects a Y-shaped chitinized support which has been commonly called the furca. For con-



venience in description and as an aid in tracing the development of the parts of the furca thruout the order, it has been divided into furca-1, which is the stem of the Y, furca-2, which is the dorsal arm of the Y, and furca-3, which is the ventral arm. The furca articulates with a small sclerite which is located between the proximal end of furca-1 and the distal end of the chitinized furrow on the meson of the theca. This piece has been called the sigma ( $\sigma$ ). Another small, independent sclerite is located in the membrane just laterad of the sigma and this may be known as kappa ( $\kappa$ ). Each paraglossa has on its mesal aspect two trachea-like structures which arise from the proximal portion of the glossa. These structures are commonly called pseudotracheae ( $\psi$ ).

A general survey of the characteristics of the paraglossae of the various labia shows that they are usually bulb-like, membranous, and somewhat flexible. In these respects they differ decidedly from the firmly chitinized, flap-like labia of many generalized insects. Their size and shape vary greatly, as can be seen in *Bibio* (Fig. 364), *Leia* (Fig. 368), *Promachus* (Fig. 376), *Geranomyia* (Fig. 382), *Tipula* (Fig. 384), *Tabanus* (Fig. 390), *Conops* (Fig. 417), *Empis* (Fig. 421), *Siphona* (Fig. 458), *Musca* (Fig. 467), *Stomoxys* (Fig. 479), and *Olfersia* (Fig. 488). The use to which the labia are put seems to have some influence on their form. The main line of development thruout the genera figured is toward the type found among the Calyptratae, in which the labia are usually large, decidedly membranous, and joined together on the dorso-caudal areas, as in *Hydrotaea* (Fig. 475), *Sarcophaga* (Fig. 477), *Sepsis* (Fig. 439), *Loxocera* (Fig. 461), *Tetanocera* (Fig. 463), and many other genera.

The membranous development of the paraglossae is not always a good indication of the main line of specialization. In a number of scattered genera, *Chironomus*, *Rhyphus*, *Aphiochaeta*, *Chloropisca*, *Platypeza*, *Leptis*, *Psilocephala*, and *Lonchoptera*, it is next to impossible to make out the chitinized pieces, such as kappa, sigma, and furca, because of the membranous condition of the entire labium. Outside of the above-named forms, the chitinized pieces of the paraglossae are usually distinct when present. These supports may be secondary in origin or they may be remnants of former chitinized parts of the paraglossae. It is possible to show how the various chitinized pieces of the majority of the labia may have been developed from the typical form.

The sclerite designated as kappa ( $\kappa$ ) on the typical labium is only present in *Tabanus* (Fig. 390 and 391), *Tipula* (Fig. 388), and *Bittacomorpha* (Fig. 85). No other dipteran gives any evidence whatever of such a sclerite. In the above-mentioned genera the pieces are embedded in the membrane laterad of the ventral ends of the theca. Some

one has interpreted these pieces as rudimentary palpigera or palpi. This may or may not be correct. It is possible for palpi to be in such a position; but since no other genera have similar pieces, and since they are so decidedly dissimilar to the labial palpi and palpigera of generalized insects, they are here regarded as secondary sclerites.

The sclerite designated as sigma ( $\sigma$ ) is present as a chitinized thickening at the ventral end of the theca, as in *Eristalis* (Fig. 443), or as a distinct piece, as in a majority of the *Brachycera* and the *Cyclorrhapha*. In all genera it is situated between the ventral margin of the theca and the furca. Only a few genera of the *Nematocera*, such as *Tipula* (Fig. 388) and *Psorophora* (Fig. 380), have these sclerites. They undergo some modification in size and structure as can be seen in the following genera: *Tabanus* (Fig. 391), *Mydas* (Fig. 397), *Conops* (Fig. 418), *Borborus* (Fig. 437), *Eristalis* (Fig. 443), *Coelopa* (Fig. 448), and *Scatophaga* (Fig. 470).

The furca of *Bibio* (Fig. 315) and that of *Tabanus* (Fig. 317) closely resemble the typical form. In *Bibio*, furca-1 (f-1) and furca-2 (f-2) are one continuous piece, while furca-3 (f-3) is a distinct arm. In *Tabanus*, furca-2 and furca-3 are distinctly chitinized areas arising from the distal end of furca-1. Only one chitinized support is present in *Sciara* (Fig. 314), *Rhabdophaga* (Fig. 313), *Psychoda* (Fig. 318), *Stratiomyia* (Fig. 331), and *Trichocera* (Fig. 311). In *Trichocera* this support has a decided dorsal bend near the constriction of the paraglossae. This bend is also present in *Psychoda* and *Stratiomyia*, but the constriction is wanting. The distal portion of the furca beyond the bend is homologous with furca-2, and furca-3 is wanting in these forms. Furca-2 is present and furca-3 is wanting in *Scenopinus* (Fig. 325); furca-3, however, is present in more species than furca-2. Such is the case with *Borborus* (Fig. 342), *Chrysomya* (Fig. 341), *Coelopa* (Fig. 337), *Tetanocera* (Fig. 344), *Scatophaga* (Fig. 357), *Musca* (Fig. 351), and *Thelaira* (Fig. 346).

Furca-1 (f-1) varies considerably thruout the order. In generalized forms where the dorso-caudal portions of the paraglossae are not joined together the furcae are always well separated. They are also separated in some forms where the paraglossae are joined, as in *Mydas* (Fig. 397) and *Eristalis* (Fig. 443). In *Chyromyia* (Fig. 411), *Drosophila* (Fig. 454), *Tetanocera* (Fig. 463), and *Sepsis* (Fig. 439), an intermediate piece joins the mesal ends of furcae-1 while in *Sarcophaga* (Fig. 477), *Musca* (Fig. 466), *Coelopa* (Fig. 448), *Sapromyza* (Fig. 409), *Chrysomya* (Fig. 457), *Heteroneura* (Fig. 459), and *Oeciothea* (Fig. 452) furcae-1 are united and form one continuous U-shaped piece. This type of furcae is present among the *Calypttratae*. The furcae of

specialized forms, such as *Olfersia* (Fig. 488), *Conops* (Fig. 418), *Siphona* (Fig. 355), *Empis* (Fig. 421), and others, are not differentiated, since the greater part of the lateral aspects of the paraglossae is chitinized.

In the typical labium two simple trachea-like structures, commonly known as pseudotracheae (ps), arise from the proximal part of each glossa and extend onto the mesal membranous aspect of each paraglossa. These trachea-like structures are in reality small chitinized troughs which serve as conduits for the liquid food. Pseudotracheae are unique structures and peculiar to Diptera, so far as known. They are present in only a few generalized forms, but from these genera it is possible to develop the pseudotracheal arrangement and structure of the more specialized Diptera. It is consequently assumed that the pseudotracheae have probably arisen only once within the order, and that this happened some time after the group as a whole was set off as a distinct order.

The pseudotracheae (ps) of *Tipula* (Fig. 383) resemble those of the typical labium in that the two main pseudotracheae arise from each glossa and extend over the mesal membranous area of the paraglossa, one of the pseudotracheae extending caudad and the other cephalad. These ducts are secondarily branched and resemble a fern. The pseudotracheae of *Mycetophila* (Fig. 11) and *Leia* (Fig. 368) are reduced and only the caudal pseudotracheae extend over the paraglossae. The paraglossae in these genera are united along the meson and form a single large lobe. The cephalic pseudotracheae are indicated by small rudiments in *Mycetophila* (Fig. 11). The pseudotracheae in these forms resemble the typical labium in that they are simple, unbranched, chitinized troughs. From the typical labium, or from the pseudotracheae as they occur in *Tipula*, it is possible to derive the arrangement and structure of the pseudotracheae as they are found in *Tabanus* (Fig. 390) and similar forms, where two long pseudotracheal trunks (m.ps) extend cephalad and caudad from the glossae (gl) and give rise to many branches on their ventral side. These branches extend ventrad over the entire mesal area of the paraglossa (pgl). The arrangement of the pseudotracheae of most Diptera is readily derived from a form similar to *Tabanus*. The arrangement in *Scenopinus* (Fig. 400), *Psilocephala* (Fig. 403), and many of the *Calyptratae* resembles that in *Tabanus*. In such genera as *Stratiomyia* (Fig. 396), *Oeciothea* (Fig. 453), *Coelopa* (Fig. 449), and *Heteroneura* (Fig. 460) no main collecting ducts (m.ps) extend beyond the glossae. In many genera, such as *Chloropisca* (Fig. 431) and *Chyromya* (Fig. 412), no line of demarkation can be drawn between the proximal ends of the pseudotracheae and the glossae.



U-shaped or open ring-like thickenings are present in the pseudotracheae of the more specialized Diptera. They do not occur in the simple pseudotracheae of *Mycetophila* or in some of the highly specialized forms. The histological structure of a pseudotrachea has been clearly demonstrated by several workers. According to Dimmock, "The pseudotracheae on the inner surfaces of the labellae of *Musca* are cylindrical channels, sunk more or less deeply into the surfaces of the labellae according to the amount that that surface is inflated, and they open on the surface in zig-zag slits. These channels are held open by partial rings, more strongly chitinized than the rest of the membrane of the cylinder. As seen from above in *Musca*, [Fig. 485], the pseudotracheae appear to be supported by partial rings, one end of each of which is forked. . . . . The pseudotracheae of *Eristalis* are so nearly like those of *Musca* [*Calliphora*] vomitoria that I have not figured those of the former." All my observations of the histological structure of pseudotracheae agree with those made by Dimmock. Tho no attempt was made to work out the detail of the histological structure in the various genera studied, a number of interesting facts were observed. The chitinized, taenidia-like thickenings (ps.th) in *Ochthera* (Fig. 445 and 483) are large U-shaped structures which are partially embedded in the membrane. The ends of these thickenings project considerably beyond the surface of the membrane and resemble these structures in *Bombylius major* (Fig. 482), as figured by Dimmock. The pseudotracheae of *Calobata* (Fig. 446) have developed into rows of small chitinized teeth (tee).

The pseudotracheal area of the paraglossae undergoes its greatest specialization in forms in which the paraglossae assume a biting function. This biting type is brought about by the development of distinct chitinized teeth arising between the proximal ends of the pseudotracheae. Rudimentary or well-developed teeth occur in *Musca* (Fig. 467), *Sarcophaga* (Fig. 478), *Scatophaga* (Fig. 472), *Lispa* (Fig. 481), and *Stomoxys* (Fig. 480). In *Musca* the small, chitinized, so-called pre-stomal teeth (tee) are present between the proximal ends of the pseudotracheae. In *Scatophaga* and *Lispa* these teeth are large and distinct. Their greatest development occurs in *Stomoxys*, and so far as observed pseudotracheae are wanting in this form. An extensive discussion of the development and the structure of the chitinized teeth of the paraglossae has been given by Patton and Cragg (1913).

The glossae (gl) of a typical labium (Fig. 1 and 73) are two small lobes located between the proximal portions of the paraglossae distad of the furrow on the theca and at the distal end of the cephalic groove. Thruout the order the glossae are between the paraglossae and at the



distal end of the cephalic groove. They are not well-defined structures in all labia. In *Chironomus* (Fig. 371), they are two small membranous lobes, while in *Simulium* (Fig. 366), *Rhabdophaga* (Fig. 367), *Bibio* (Fig. 364), and *Rhyphus* (Fig. 374) they have the form of a single median membranous lobe. The glossae of *Simulium* are of particular interest since they have a great number of minute chitinized thickenings which radiate from the proximal end. So far as known these thickenings bear no relation to the pseudotracheae of the paraglossae. The glossae of *Tabanus* (Fig. 391) are united and form a chitinized tridentate piece with the median tooth the longest. The glossae of *Lonchop-tera* (Fig. 407) illustrate a form intermediate between a median spine, such as occurs in *Psorophora* (Fig. 381), *Aphiochaeta* (Fig. 393), *Empis* (Fig. 422), and *Exoprosopa* (Fig. 426), and the U-shaped structure characteristic of the *Cyclorrhapha*. The glossae of the *Calyptratae* resemble in general the glossae of *Musca* (Fig. 465). In the genera of this group the cephalic ends of the U-shaped piece are free and project cephalad from the point of attachment of the pseudotracheae. The glossae are not well defined in a few genera, *Sapromyza* (Fig. 410), *Chyromya* (Fig. 412), and *Chloropisca* (Fig. 431), for example, and it is impossible to differentiate the glossae from the chitinized groove of the mediproboscis and the proximal ends of the pseudotracheae. The glossae of *Promachus* (Fig. 379) are specialized in that they give rise to two thickenings which extend dorsad in the groove of the labium and serve as guides for the hypopharynx and galeae.

#### EPIPHARYNX AND HYPOPHARYNX

The anterior end of the alimentary canal of the Orthoptera and of insects in general is divided transversely into two parts, one forming the cuticular lining of the clypeus and labrum and the other the lining of the opposite side of the mouth cavity. The portion lining the clypeus and labrum is known as the epipharynx (ep), and that of the opposite side as the hypopharynx (hp). Each lining may be subdivided into several parts. These are of particular significance in a study of the epipharynx, which has a distinct chitinized mesal piece, and two lateral chitinized pieces which are situated near the clypeo-labral suture. These lateral pieces, which have been designated as tormae (to), and, so far as I know, are described here for the first time, project cephalad toward the clypeo-labral suture in *Melanoplus* (Fig. 515) and *Gryllus* (Fig. 516) and connect with both the labrum and clypeus. In *Gryllus* they are interpolated between the clypeus and the labrum and appear as small triangular sclerites on the cephalic aspect. The tormae of *Periplaneta* (Fig. 514) are not as well developed as in the above-named

genera, but they are present and project toward the cephalo-lateral corners of the labrum. The caudal end of the epipharynx in many insects gives rise to long chitinized arms which have been called cornua (cu). The hypopharynx may be subdivided into a distal, unpaired, median piece, which is usually called the hypopharynx, and a proximal paired area.

The chitinized portion of the anterior end of the alimentary canal of Diptera can be homologized with the epipharynx and the hypopharynx of generalized insects. The following hypothetical epipharynx and hypopharynx (Fig. 493) and their closely associated parts have been constructed for Diptera. In the figures of the lateral views of the hypothetical type an enlarged, three-sided, chitinized tube extends caudad from the dorsal end of the hypopharynx and epipharynx. It has been called the oesophageal pump (oe.p). This is not a part of the epipharynx or of the hypopharynx, but is a modification of the pharynx, a portion of the alimentary canal. All of the chitinized parts ventrad of the membranous area at the cephalic end of the oesophageal pump belong to the epipharynx and the hypopharynx. The dorsal ends of the epipharynx and the hypopharynx are united and form a single chitinized tube, and this has been called the basipharynx (bph). Except for this union, the epipharynx and the hypopharynx are continuous chitinized pieces with lance-like distal ends. The distal portion of the epipharynx is joined to the labrum by a membrane along its lateral margin. The tormae in the hypothetical type project from the lateral margins of the epipharynx and unite with the latero-ventral portions of the fronto-clypeus (fr.c). Two projections occur at the dorsal end of the basipharynx, and these are considered homologous with the cornua (cu) of the epipharynx of generalized insects. The distal end of the hypopharynx is a free lance-like organ, and a salivary duct (s.d) enters its proximal end just dorsad of the place where it joins the labium (li). The salivary duct extends thru the hypopharynx to its distal end.

The oesophageal pump of the alimentary canal is closely associated with the epipharynx and hypopharynx in all the Nematocera and in *Promachus* (Fig. 517), *Tabanus* (Fig. 494), *Leptis* (Fig. 520), and *Psilocephala* (Fig. 533) of the Brachycera. In a majority of the above forms, the oesophageal pump is an elastic, semi-chitinized, three-sided tube with muscles connecting with each of its surfaces. A contraction of these muscles expands the tube, which upon their relaxation assumes its normal shape. In some forms, as *Tabanus* and *Promachus*, there is only one chitinized elastic surface. In a number of genera, as *Chironomus* (Fig. 531), *Psychoda* (Fig. 529), and *Leptis* (Fig. 520), the

tube is more or less membranous and not distinctly three-sided. The oesophageal pump is wanting in all the Diptera except those named, and the membranous oesophagus connects directly with the basipharynx. The oesophageal pump shows considerable variation in its shape, position, and size, as can be seen in the figures of *Bibio* (Fig. 523), *Rhyphus* (Fig. 508) and others.

The basipharynx (bph) is interpreted as including all of the united portions of the epipharynx and the hypopharynx, but the extent of this union varies somewhat in the different genera. In a majority of the Nematocera no sutures or constrictions occur between the basipharynx and the lance-like portions of the epipharynx and the hypopharynx. Such constrictions and secondary sutures do occur in a majority of the Brachycera, as in *Leptis* (Fig. 520) and *Promachus* (Fig. 517), and in all of the Cyclorrhapha. The basipharynx (bph) varies in size and shape, as can be seen in the figures. Muscles connect with the cephalic and caudal aspects of the basipharynx, those on the cephalic aspect expanding the basipharynx and thus producing suction. This sucking apparatus is well developed in all forms which have no oesophageal pump. The chitinized projections at the dorsal end of the basipharynx, called the cornua (cu), vary in shape and size. Some are blunt, others long and narrow, as in *Leptis* and the Calyptratae, and still others are disk-shaped, as in *Promachus* (Fig. 517).

Distinct tormae (to) are present in Diptera except in a few species of the Nematocera. In all the Nematocera and in *Leptis* (Fig. 520), *Psilcephala* (Fig. 533), *Platypeza* (Fig. 543), *Aphiochaeta* (Fig. 544), *Lonchoptera* (Fig. 539), and *Scenopinus* (Fig. 538), they resemble the hypothetical type in that they join with the fronto-clypeus. In other genera the tormae have an exposed portion located ventrad of the fronto-clypeus and all connection between the fronto-clypeus and the tormae is lost, except in *Simulium* (Fig. 497) and *Tabanus*. The variations in the shape and the extent of the tormae is well illustrated by the numerous figures. The so-called fulcrum described by numerous morphologists for the Calyptratae is composed of the tormae and the basipharynx. A more or less distinct secondary suture (s.s) is shown in the drawings as separating the tormae from the basipharynx, and the broken line on the tormae indicates the place of connection of the membrane of the basiproboscis with the tormae. In figures of the Nematocera and of forms in which the tormae connect with the fronto-clypeus the broken line indicates the place of union between these parts.

The epipharynx (ep) is present and closely associated with the labrum in all Diptera having functional mouth-parts. The interrelationship between the epipharynx and the labrum has been discussed



under the heading labrum. The epipharynx in a number of generalized Diptera, such as *Tabanus* (Fig. 494), *Simulium* (Fig. 497), *Dixa* (Fig. 501), *Limnobia* (Fig. 507), and *Sciara* (Fig. 513), resembles the hypothetical type. In the majority of the Diptera it differs from the hypothetical type in that it is completely separated from the basipharynx by a constriction or a secondary suture. This hinge in the epipharynx permits the proboscis to bend at this point when it is withdrawn into the oral cavity. The lance-like portion of the epipharynx in the Calyptratae and some other forms is completely separated from the basipharynx by the development of a special piece which is commonly called the hyoid (hy). The lance-like portion of the hypopharynx also articulates against the hyoid. The hyoid is a secondary sclerite which originated from the epipharynx or the hypopharynx and serves the purpose of keeping open the alimentary canal, which passes thru it. A structure similar to the hyoid of *Musca* (Fig. 600) is found in *Stomoxys* (Fig. 599), where a large and strong trachea-like tube extends between the dorsal ends of the lance-like portions of the epipharynx, the hypopharynx, and the basipharynx.

In size and shape the epipharynx agrees more or less closely with the labrum. The epipharynx in sucking Diptera is, as a rule, long and needle-like, while in other forms it is usually short and blunt. In many genera of the Acalyptratae it has a secondary transverse suture near its distal end, as shown in *Sepsis* (Fig. 583) and *Eristalis* (Fig. 588).

A few genera show special modifications of the epipharynx. This is particularly true of *Dolichopus* (Fig. 524 and 528). In this genus the epipharynx closely resembles the hypothetical type in the presence of a distinct membrane between the labrum (l) and the epipharynx (ep). The specialization of the epipharynx consists in the bifurcation of its distal end and in the presence of a long club-shaped piece which projects from its meson dorsad into the cavity formed by the basipharynx, the tormae, and the fronto-clypeus. These modifications are peculiar to species of the Dolichopodidae. The bifurcations at the distal end are of particular interest, since they have been interpreted as mandibles by Langhoffer (1888). They are much longer in some of the genera of the family than in others. The lateral and caudal views of the epipharynx and the hypopharynx of *Dolichopus* show clearly the relation these projections have to the other parts, and justify the interpretation here given.

The single, median, distal, lance-like portion of the hypopharynx is present in all but a few of the genera studied. The cephalic portion of the labium usually connects with the lance-like portion of the hypopharynx just ventrad of the point of entrance of the salivary duct.



In a few cases, as in *Borborus* (Fig. 565 and 567), the hypopharynx is completely fused with the labium, while in others, as in *Euaresta* (Fig. 572), it is nearly so. In a majority of the genera the secondary separation of the lance-like portion of the hypopharynx from the basipharynx corresponds with the similar separation in the epipharynx. The shape and size of the hypopharynx also vary considerably, as can be seen in the figures. In mouth-parts fitted for sucking and piercing, the hypopharynx is usually long and needle-like; while in licking forms (most *Calyptratae*), it is greatly reduced.

The salivary duct (s. d) enters the proximal portion of the lance-like part of the hypopharynx and in most cases it is carried as a duct or groove along the cephalic surface of that organ to the distal end. The course of this duct or groove is indicated by broken lines in the figures of the caudal aspect of the hypopharynx. The salivary duct before entering the hypopharynx is enlarged and bulb-like in many species. In *Tabanus* (Fig. 494) the salivary bulb (s. b) is a chitinized structure continuous with the hypopharynx, while in *Promachus* (Fig. 517) it is chitinized, but separated from the hypopharynx. A chitinized bulb and an enlarged membranous swelling are both present in *Dolichopus* (Fig. 528).

The peculiar epipharynx and hypopharynx of *Olfersia* (Fig. 606) can be homologized with the more common types found thruout the order. The principal difference is in the shape and position of the basipharynx, the tormae, and the hyoid. The two lance-like structures embedded in the deep membranous depression about the oral cavity are the labrum-epipharynx and the lance-like part of the hypopharynx. The long, crescent-shaped piece which extends cephalad from the proximal end of the labrum-epipharynx to the pear-shaped piece, is homologous with the hyoid (hy), and the pear-shaped piece with which the hyoid connects is composed of the tormae (to) and the basipharynx (bph). The exposed parts of the tormae in the membrane ventrad of the head are very small in this genus.

Only rudiments of mouth-parts are found in the head of *Gastrophilus* (Fig. 490 and 492). The anterior end of the alimentary canal is a simple chitinized tube which leads to the small opening on the ventral aspect of the head. This tube undoubtedly originated from the epipharynx and the hypopharynx. The mouth-parts are greatly reduced or wanting. It is possible that the small bulb-like structures located latero-caudad of the opening are remnants of the labium. It is impossible to homologize the other minute modifications surrounding the mouth-opening.

In the *Cyrtidae*, as *Oncodes* (Fig. 109, 486, and 487), the mouth-

parts show a greater reduction than in *Gastrophilus*, while in species of *Eulonchus* (Fig. 364a) they are well developed. In *Oncodes* a chitinized ring is present in the membrane which covers the oral cavity, and a broad plate extends dorsad from its caudal margin, giving rise to a small membranous tube, the oesophagus, which has no opening to the exterior as far as could be determined. It is impossible to homologize the parts within the oral cavity. The ental plate which gives rise to the oesophagus, may be homologous with the basal portion of the epipharynx and the hypopharynx.

A general survey of the epipharynx and hypopharynx shows that the relationship between these parts and the head-capsule corresponds with the relationship between the mouth-parts and the head. Since the epipharynx and the hypopharynx are always connected with the labrum and the proximal part of the labium, they are projected ventrad when the labrum and labium are extruded. The interrelation of the mouth-parts and the epipharynx and hypopharynx is fixed, never changing thruout the order, no matter what specialization may take place. The especially striking feature of the epipharynx and the hypopharynx in various genera which have functional mouth-parts, is the decided similarity of the two thruout the order, as shown by the various figures. The parts undergo secondary changes in their size and shape, but in no case where the mouth-parts are functional is there an entire loss of a part, which, however, happens in many cases with the mouth-appendages. The epipharynx and hypopharynx of the Calyptratae in particular show a development of joints, secondary sclerites, and membranous areas, which permit a considerable amount of flexibility.

### SUMMARY

This investigation deals with the homology of all the sclerites of the fixed and movable parts of the head of one or more representatives of fifty-three of the fifty-nine families of the Diptera of North America as listed by Aldrich. With this large series it has been possible to make clear a number of little-understood relationships and structural modifications in the head and mouth-parts, and also to point out their homology with the corresponding parts and areas in insects of other orders. The six hundred and more figures show the form and structure of all the parts for each of the families studied.

Modifications of the fixed and movable parts usually take the form of reduction, change of shape, loss of chitination, or expansion of the membranous areas. The different parts have been discussed separately, and a hypothetical or typical form has been constructed for each part.

One of the most important conclusions concerning the generalized head-capsule relates to the position of the epicranial suture. The stem of this suture along the dorso-meson represents the line of fusion of the paired sclerites of the head, while the arms of the suture ventrad of the antennal fossae enclose the unpaired sclerites of the head. This suture resembles the epicranial suture in the immature stages and the adult forms of all the generalized members of the more common orders.

Two unpaired sclerites, front and clypeus, are enclosed by the fork of the epicranial suture, and in all but one or two genera form a continuous area called the fronto-clypeus.

The labrum is an unpaired, distinct, tongue-like structure situated ventrad of the fronto-clypeus. It is joined to the epipharynx and the resulting structure is known as the labrum-epipharynx.

The tormae are chitinized lateral pieces of the epipharynx which project cephalad and unite with the fronto-clypeus in generalized Diptera. They are also present in such generalized insects as the Orthoptera. In the more specialized Diptera the tormae are interpolated between the fronto-clypeus and the labrum, and in all but a few genera lose all connection with the chitinized portions of the fronto-clypeus. Their exposed surface is best seen from a cephalic view.

The crescent-shaped frontal suture dorsad of the antennal fossae marks the line of invagination of the ptilinum. The origin of the ptilinum has not been determined.

The vertex is the paired continuous area on the cephalic aspect of the head, and the region of the vertex ventrad and mesad of each compound eye is a gena.

The compound eyes are usually large and located on the cephalolateral aspects of the head. They show secondary sexual characters in a greater number of species than do any other of the fixed and movable parts. The three ocelli are arranged in the form of a triangle and located on the vertex dorsad of the bifurcation of the arms of the epicranial suture.

The occiput and postgenae are continuous areas of the caudal surface. The former occupies the dorsal portion and is secondarily modified about the occipital foramen to form the parocciput. The postgenae are the two areas of the ventral half, separated by a membrane in generalized forms and united ventrad of the occipital foramen in all the Brachycera and the Cyclorrhapha. They are also secondarily divided into parapostgenae along the mesal membrane.

The tentorium of generalized Diptera is represented by the usual three pairs of arms and a rudimentary body. It undergoes striking modifications, and influences to a considerable extent the detailed struc-



ture of the head. The relation between the invaginations of the tentorium and the movable appendages of the mouth, which is so important a feature of all generalized insects, is also characteristic of the members of this order.

The development of the antennae from a generalized filiform type to that found among the Cyclorrhapha can be traced on the figures.

Only a few generalized Diptera have mandibles. These are only present in the females except in *Simulium*, in which they are well developed in both sexes.

All Diptera having functional mouth-parts have maxillae. The maxillae of generalized Diptera resemble the maxillae of generalized insects except for the absence of palpifers and the fusion of the cardines and stipites with the head-capsule. The maxillae undergo considerable modification, and are reduced to a mere ental rod and a palpus in the Calyptratae.

The labium is the most characteristic and specialized appendage of the mouth, and shows modifications due to reduction and membranous development. The palpifers and labial palpi are always wanting. The submentum and mentum are represented by a membranous area of the caudal surface of the head. The ligula, or the movable portion of the labium, has a basal part which usually gives rise to two large bulb-like paraglossae and to glossae situated between them. The paraglossae are specialized, and have chitinized areas on their lateral and caudal surfaces and pseudotracheae on their mesal surface.

The parts of the epipharynx and the hypopharynx can be homologized with the corresponding parts in generalized insects. There is a great similarity in the form of the epipharynx and hypopharynx of all Diptera, which is especially striking when considered in connection with the modifications that have taken place in all other parts.

The various mouth-parts show striking modifications thruout the order, but all, including the epipharynx and the hypopharynx, retain their relative positions, even tho they may be extruded from the head-capsule for a considerable distance, as in some of the Calyptratae. The proboscis of the Cyclorrhapha is composed of the labium, maxillae, hypopharynx, labrum-epipharynx, and tormae. The paraglossae of the labium form the large lobes, or labellae, at its distal end.

The mouth-parts of *Oncodes* and *Gastrophilus* are not functional, and are so greatly reduced that it is difficult to homologize their parts.



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## EXPLANATION OF PLATES

## ABBREVIATIONS USED

a.a	Anterior arms of the tentorium	i.a.d	Invagination of the anterior and dorsal arms of the tentorium
a.e.s	Arms of the epicranial suture	i.d	Invagination of the dorsal arm of the tentorium
a.f	Antennal fossa	i.p	Invagination of the posterior arm of the tentorium
al.c	Alimentary canal	k	Kappa (sclerite)
ant	Antenna	l	Labrum
ar	Arista	la	Lacinia
a.s	Antennal sclerite	le	Labella
bph	Basipharynx	lep	Labrum epipharynx
bpr	Basiproboscis	lg	Ligula
b.t	Body of the tentorium	li	Labium
c	Clypeus	m	Membrane
ca	Cardo	md	Mandible
c.e	Compound eye	me	Mentum
ch	Chitinized	mpr	Mediproboscis
ch.th	Chitinized thickening	m.ps	Main pseudotracheae
c.l.s	Clypeo-labral suture	mx	Maxilla
cu	Cornu	mx.pl	Maxillary palpus
d.a	Dorsal arms of the tentorium	n.s	Neck sclerite
de	Depression	oc	Ocellus
dpr	Distiproboscis	oc.a	Ocellar area
ep	Epipharynx	occ	Occiput
e.s	Epicranial suture	oe	Oesophagus
f	Furca, also f-1, f-2, and f-3	oe.p	Oesophageal pump
fa	Facet	o.f	Occipital foramen
fl	Flagellum	o.l	Oral lobe
fr	Front	o.s	Ocular sclerite
fr.c	Fronto-clypeus	p.a	Posterior arms of the tentorium
fr.s	Frontal suture	pd	Pedicel
g	Galea	pgl	Paraglossa
ge	Gena	po	Postgena
gl	Glossa	pocc	Parocciput
h	Hook	ppo	Parapostgena
hp	Hypopharynx	pr	Proboscis
hy	Hyoid		
i.a	Invagination of the anterior arm of the tentorium		

ps	Pseudotrachea	so	Sense organ
ps.th	Pseudotracheal thickening	s.s	Secondary suture
pt	Ptilinum	st	Stipes. st-1 and st-2 ectal part,
r.d.a	Rudimentary dorsal arms of the tentorium	st-e	ental part
r.p.a	Rudimentary posterior arms of the tentorium	su	Submentum
s	Suture	su.me	Submentum and mentum
s.b	Salivary bulb	t	Tentorium
sc	Scape	tee	Teeth-like structures
s.d	Salivary duct	th	Thickening
s.e.s	Stem of the epicranial suture	the	Theca
si	Sigma (sclerite)	to	Torma or tormae
		t.th	Tentorial thickening
		v	Vertex

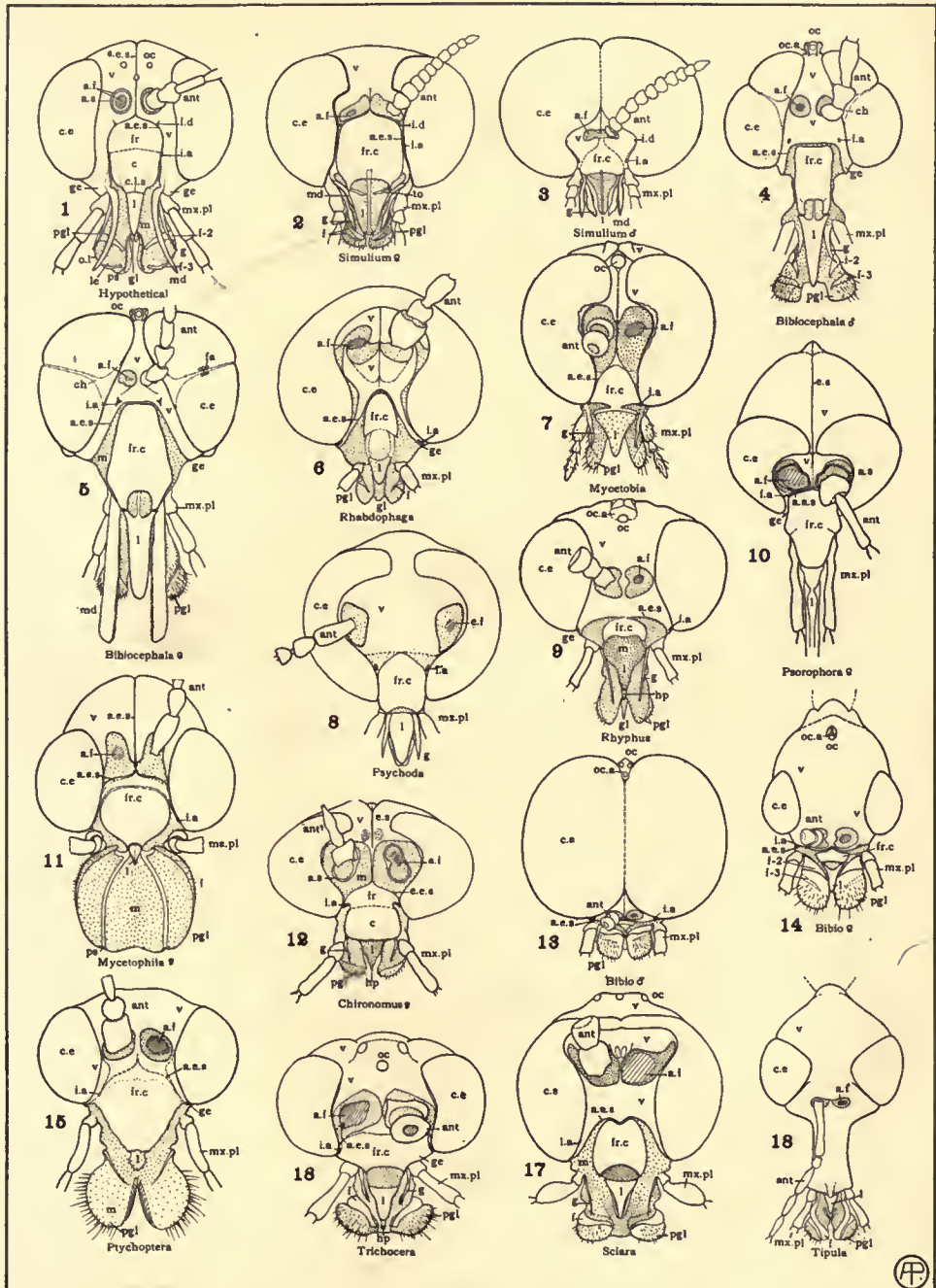


## PLATE I

## EXPLANATION OF PLATE

## CEPHALIC ASPECT OF THE HEAD AND MOUTH-PARTS

- Fig. 1. Hypothetical head.
- Fig. 2. *Simulium venustum*, female.
- Fig. 3. *Simulium johannseni*, male.
- Fig. 4. *Bibliocephala elegantula*, male.
- Fig. 5. *Bibliocephala elegantula*, female.
- Fig. 6. *Rhabdophaga strobiloides*.
- Fig. 7. *Mycetobia divergens*.
- Fig. 8. *Psychoda albipennis*.
- Fig. 9. *Rhyphus punctatus*.
- Fig. 10. *Psorophora ciliato*, female.
- Fig. 11. *Mycetophila punctata*, female.
- Fig. 12. *Chironomus ferrugineovittatus*, female.
- Fig. 13. *Bibio femoratus*, male.
- Fig. 14. *Bibio femoratus*, female.
- Fig. 15. *Ptychoptera rufocincta*.
- Fig. 16. *Trichocera bimacula*.
- Fig. 17. *Sciara varians*.
- Fig. 18. *Tipula bicornis*.





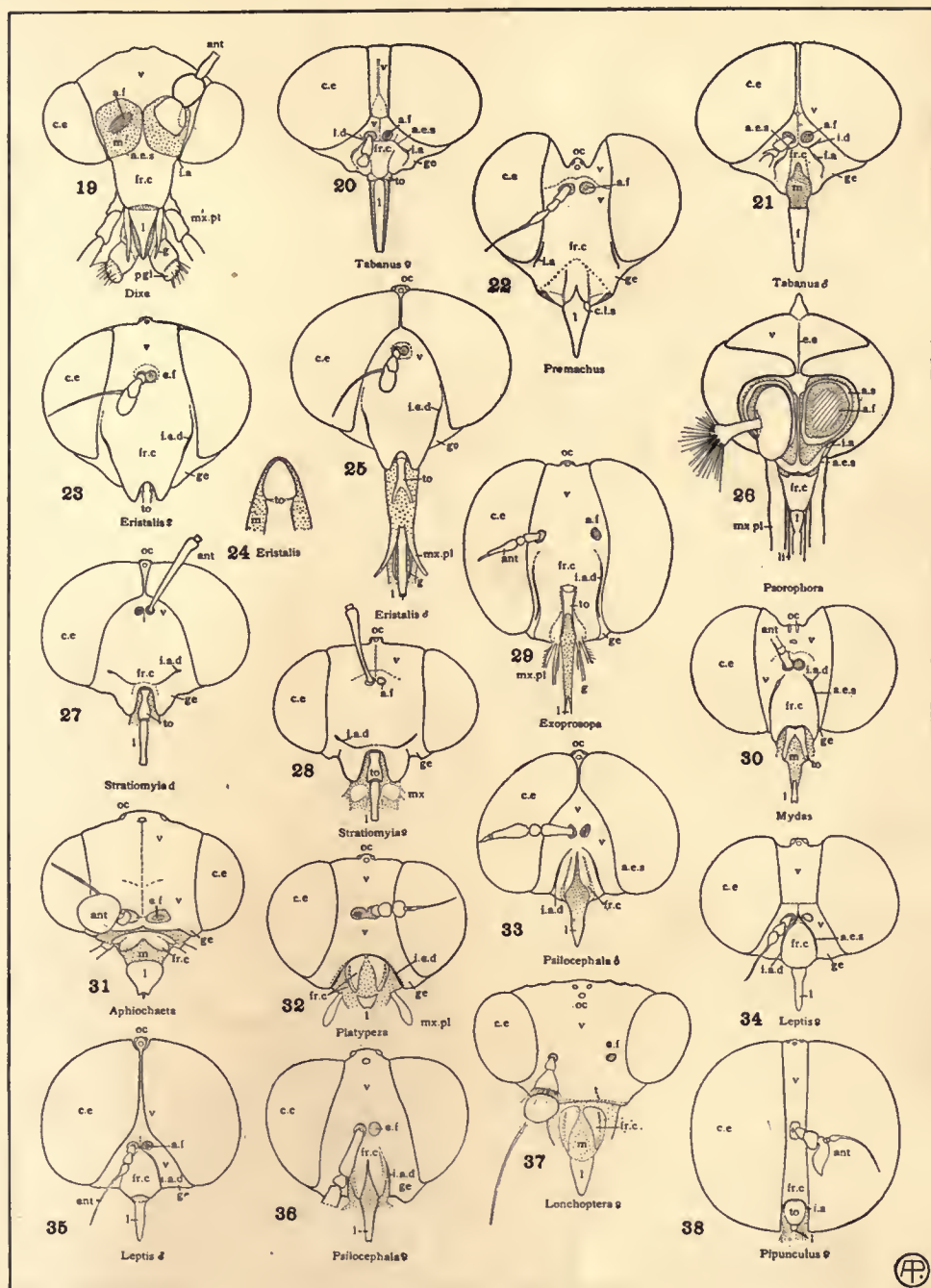


## PLATE II

## EXPLANATION OF PLATE

## CEPHALIC ASPECT OF THE HEAD

- Fig. 19. *Dixa clavata*.
- Fig. 20. *Tabanus giganteus*, female.
- Fig. 21. *Tabanus giganteus*, male.
- Fig. 22. *Promachus vertebratus*.
- Fig. 23. *Eristalis tenax*, female.
- Fig. 24. *Eristalis tenax*, dorsal end of the tormae.
- Fig. 25. *Eristalis tenax*, male.
- Fig. 26. *Psorophora ciliata*, male.
- Fig. 27. *Stratiomyia apicula*, male.
- Fig. 28. *Stratiomyia apicula*, female.
- Fig. 29. *Exoprosopa fasciata*.
- Fig. 30. *Mydas clavatus*.
- Fig. 31. *Aphiochaeta agarici*.
- Fig. 32. *Platypeza velutina*.
- Fig. 33. *Psilocephala haemorrhoidalis*, male.
- Fig. 34. *Leptis vertebrata*, female.
- Fig. 35. *Leptis vertebrata*, male.
- Fig. 36. *Psilocephala haemorrhoidalis*, female.
- Fig. 37. *Lonchoptera lutea*, female.
- Fig. 38. *Pipunculus cingulatus*, female.





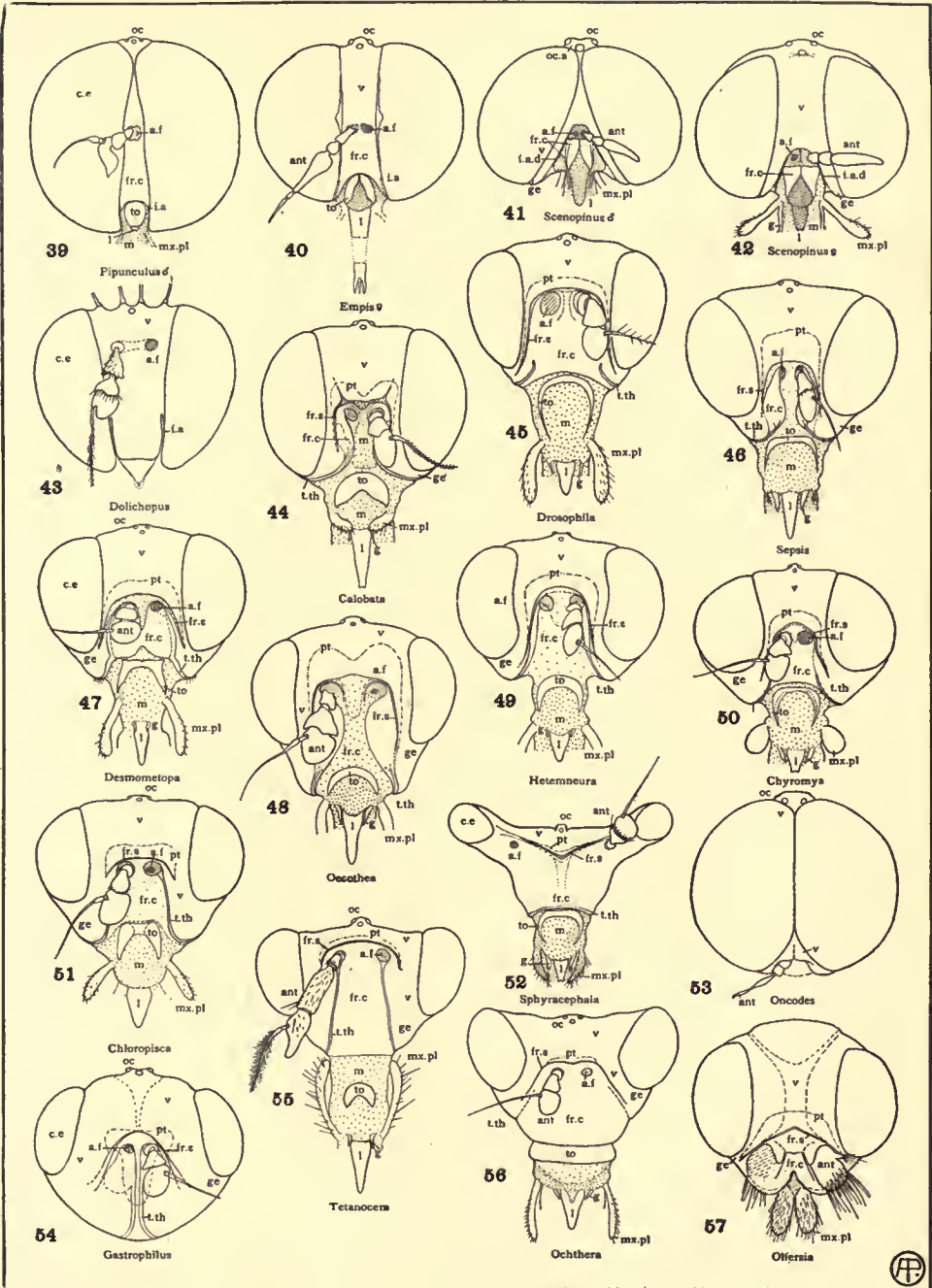


## PLATE III

## EXPLANATION OF PLATE

## CEPHALIC ASPECT OF THE HEAD

- Fig. 39. *Pipunculus cingulatus*, male.
- Fig. 40. *Empis clausa*, female.
- Fig. 41. *Scenopinus fenestralis*, male.
- Fig. 42. *Scenopinus fenestralis*, female.
- Fig. 43. *Dolichopus bifractus*.
- Fig. 44. *Calobata univitta*.
- Fig. 45. *Drosophila ampelophila*.
- Fig. 46. *Sepsis violacea*.
- Fig. 47. *Desmometopa latipes*.
- Fig. 48. *Oecothia fenestralis*.
- Fig. 49. *Heteroneura flaviseta*.
- Fig. 50. *Chyromya concolor*.
- Fig. 51. *Chloropisca glabra*.
- Fig. 52. *Sphyracephala brevicornis*.
- Fig. 53. *Oncodes costatus*.
- Fig. 54. *Gastrophilus equi*.
- Fig. 55. *Tetanocera plumosa*.
- Fig. 56. *Ochthera mantis*.
- Fig. 57. *Olfersia ardeae*.





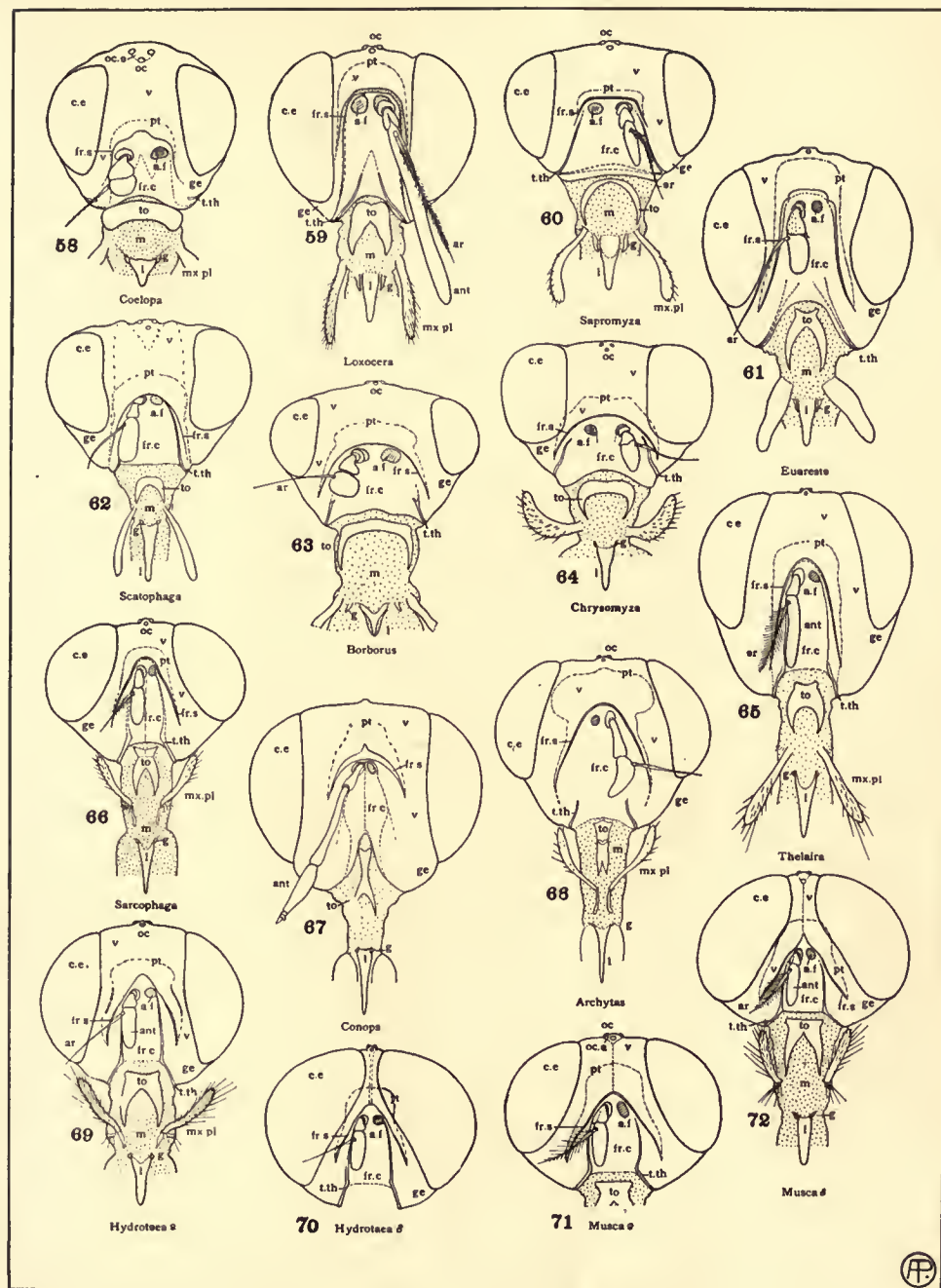


## PLATE IV

## EXPLANATION OF PLATE

## CEPHALIC ASPECT OF THE HEAD

- Fig. 58. *Coelopa vanduzeei*.  
Fig. 59. *Loxocera pectoralis*.  
Fig. 60. *Sapromyza vulgaris*.  
Fig. 61. *Euaresta aequalis*.  
Fig. 62. *Scatophaga furcata*.  
Fig. 63. *Borborus equinus*.  
Fig. 64. *Chrysomya demandata*.  
Fig. 65. *Thelaira leucozona*.  
Fig. 66. *Sarcophaga haemorrhoidalis*.  
Fig. 67. *Conops brachyrhynchus*.  
Fig. 68. *Archytas analis*.  
Fig. 69. *Hydrotaea dentipes*, female.  
Fig. 70. *Hydrotaea dentipes*, male.  
Fig. 71. *Musca domestica*, female.  
Fig. 72. *Musca domestica*, male.





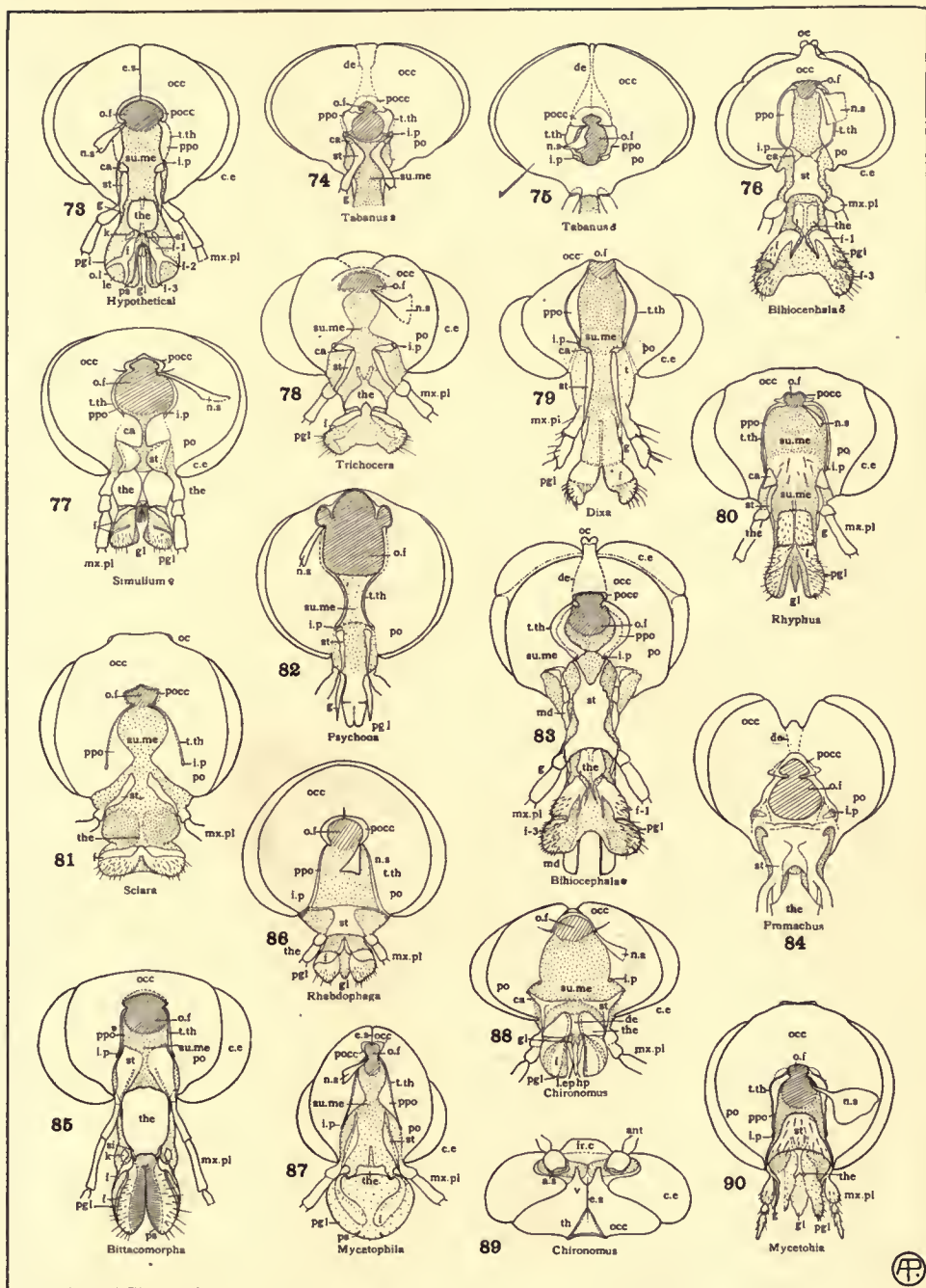


## PLATE V

## EXPLANATION OF PLATE

## CAUDAL ASPECT OF THE HEAD

- Fig. 73. Hypothetical head.  
Fig. 74. *Tabanus giganteus*, female.  
✓ Fig. 75. *Tabanus giganteus*, male.  
Fig. 76. *Bibliocephala elegantula*, male.  
Fig. 77. *Simulium venustum*, female.  
Fig. 78. *Trichocera bimaculata*.  
Fig. 79. *Dixa clavata*.  
Fig. 80. *Rhyphus punctatus*.  
Fig. 81. *Sciara varians*.  
Fig. 82. *Psychoda albipennis*.  
Fig. 83. *Bibliocephala elegantula*, female.  
Fig. 84. *Promachus vertebratus*.  
Fig. 85. *Bittacomorpha clavipes*.  
Fig. 86. *Rhabdophaga strobiloides*.  
Fig. 87. *Mycetophila punctata*.  
Fig. 88. *Chironomus ferrugineovittatus*.  
Fig. 89. *Chironomus ferrugineovittatus*, dorsal aspect.  
Fig. 90. *Mycetobia divergens*.





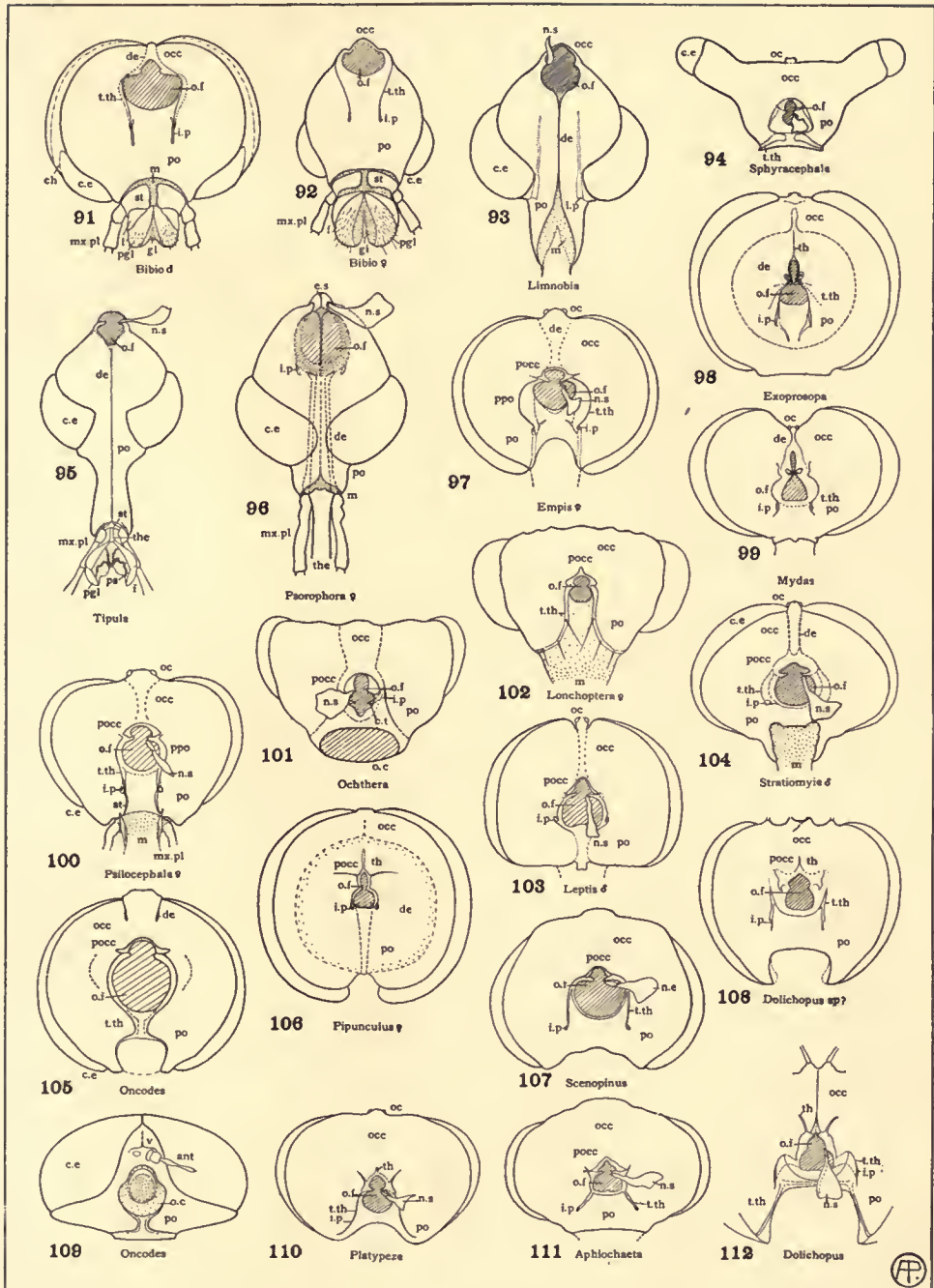


## PLATE VI

## EXPLANATION OF PLATE

## CAUDAL ASPECT OF THE HEAD

- Fig. 91. *Bibio femoratus*, male.
- Fig. 92. *Bibio femoratus*, female.
- Fig. 93. *Linnobia immatura*.
- Fig. 94. *Sphyracephala brevicornis*.
- Fig. 95. *Tipula bicornis*.
- Fig. 96. *Psorophora ciliata*, female.
- Fig. 97. *Empis clausa*, female.
- Fig. 98. *Exoprosopa fasciata*.
- Fig. 99. *Mydas clavatus*.
- Fig. 100. *Psilocephala haemorrhoidalis*, female.
- Fig. 101. *Ockthera mantis*.
- Fig. 102. *Lonchoptera lutea*, female.
- Fig. 103. *Leptis vertebrata*, male.
- Fig. 104. *Stratiomyia apicula*, male.
- Fig. 105. *Oncodes costatus*.
- Fig. 106. *Pipunculus cingulatus*, female.
- Fig. 107. *Scenopinus fenestralis*.
- Fig. 108. *Dolichopus* sp.
- Fig. 109. *Oncodes costatus*, ventral aspect.
- Fig. 110. *Platypeza velutina*.
- Fig. 111. *Aphiochaeta agarici*.
- Fig. 112. *Dolichopus bifracius*, lateral margins incomplete.





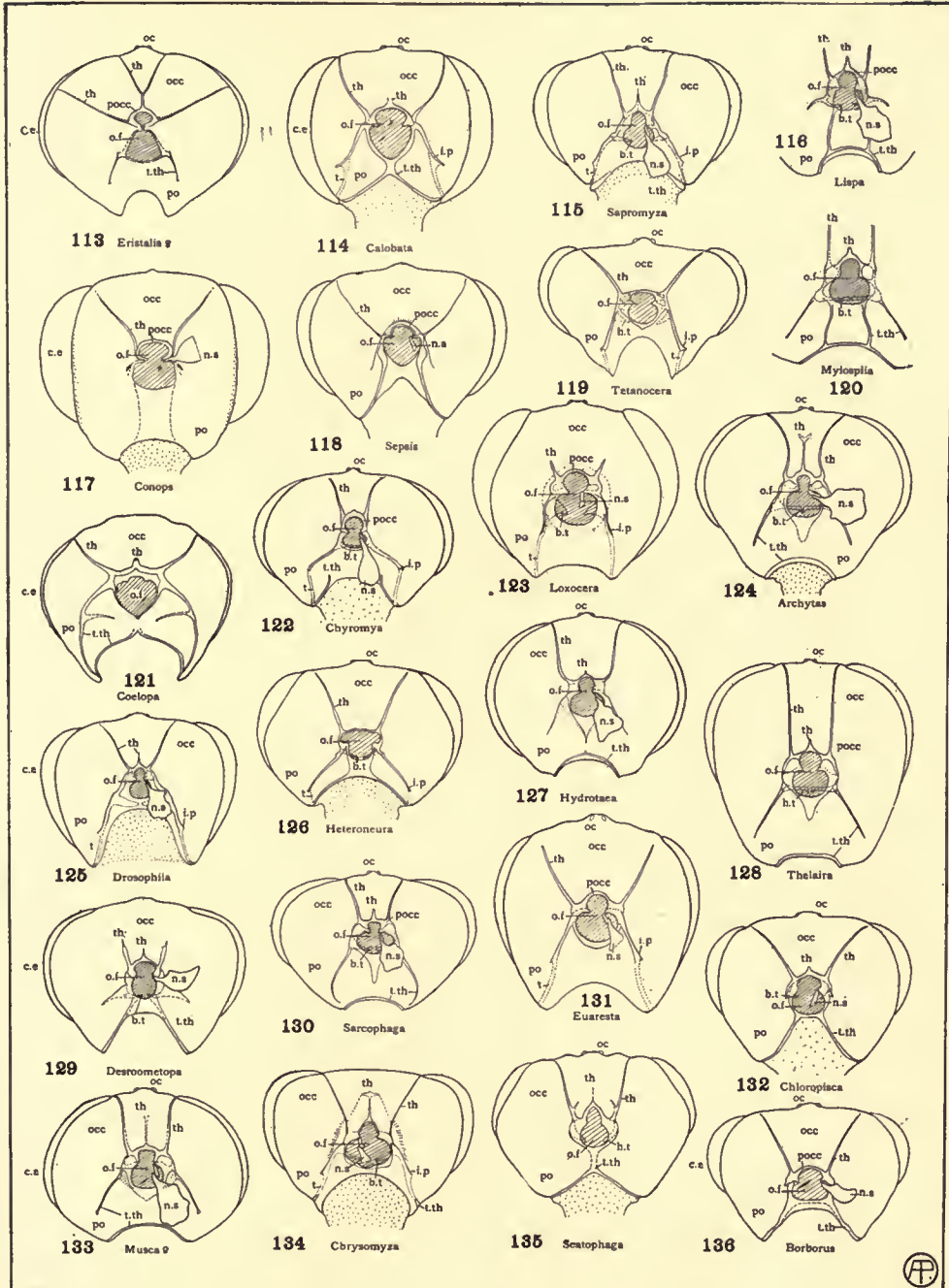


## PLATE VII

## EXPLANATION OF PLATE

## CAUDAL ASPECT OF THE HEAD

- Fig. 113. *Eristalis tenax*, female.  
Fig. 114. *Calobata univitta*.  
Fig. 115. *Sapromyza vulgaris*.  
Fig. 116. *Lispa nasoni*, margin incomplete.  
Fig. 117. *Conops brachyrhynchus*.  
Fig. 118. *Sepsis violacea*.  
Fig. 119. *Tetanocera plumosa*.  
Fig. 120. *Myiospila meditabunda*, margin incomplete.  
Fig. 121. *Coelopa vanduzeei*.  
Fig. 122. *Chiromya concolor*.  
Fig. 123. *Loxocera pectoralis*.  
Fig. 124. *Archytas analis*.  
Fig. 125. *Drosophila ampelophila*.  
Fig. 126. *Heteroneura flaviseta*.  
Fig. 127. *Hydrotaea dentipes*.  
Fig. 128. *Thelaira leucozona*.  
Fig. 129. *Desmometopa latipes*.  
Fig. 130. *Sarcophaga haemorrhoidalis*.  
Fig. 131. *Euaresta aequalis*.  
Fig. 132. *Chloropisca glabra*.  
✓ Fig. 133. *Musca domestica*, female.  
Fig. 134. *Chrysomya demandata*.  
Fig. 135. *Scatophaga furcata*.  
Fig. 136. *Borborus equinus*.







## PLATE VIII

## EXPLANATION OF PLATE

## CAUDAL AND LATERAL ASPECTS OF THE HEAD AND THE TENTORIUM

- Fig. 137. *Oecotheca fenestralis*, caudal aspect.
- Fig. 138. *Gastrophilus equi*, caudal aspect.
- Fig. 139. *Olfersia ardeae*, caudal aspect.
- Fig. 140. Hypothetical head, lateral aspect.
- Fig. 141. Hypothetical tentorium, lateral aspect.
- Fig. 142. *Tabanus giganteus*, female, lateral aspect.
- Fig. 143. *Tabanus giganteus*, lateral aspect of the tentorium.
- Fig. 144. *Simulium venustum*, female, lateral aspect.
- Fig. 145. *Leptis vertebrata*, male, lateral aspect.
- Fig. 146. *Mydas clavatus*, lateral aspect.
- Fig. 147. *Promachus vertebratus*, lateral aspect.
- Fig. 148. *Promachus vertebratus*, lateral aspect of the tentorium.
- Fig. 149. *Scenopinus fenestralis*, female, lateral aspect.
- Fig. 150. *Sciara varians*, lateral aspect.
- Fig. 151. *Pipunculus cingulatus*, lateral aspect.
- Fig. 152. *Chironomus ferrugineovittatus*, lateral aspect.
- Fig. 153. *Bibio femoratus*, female, lateral aspect.
- Fig. 154. *Bibio femoratus*, male, lateral aspect.

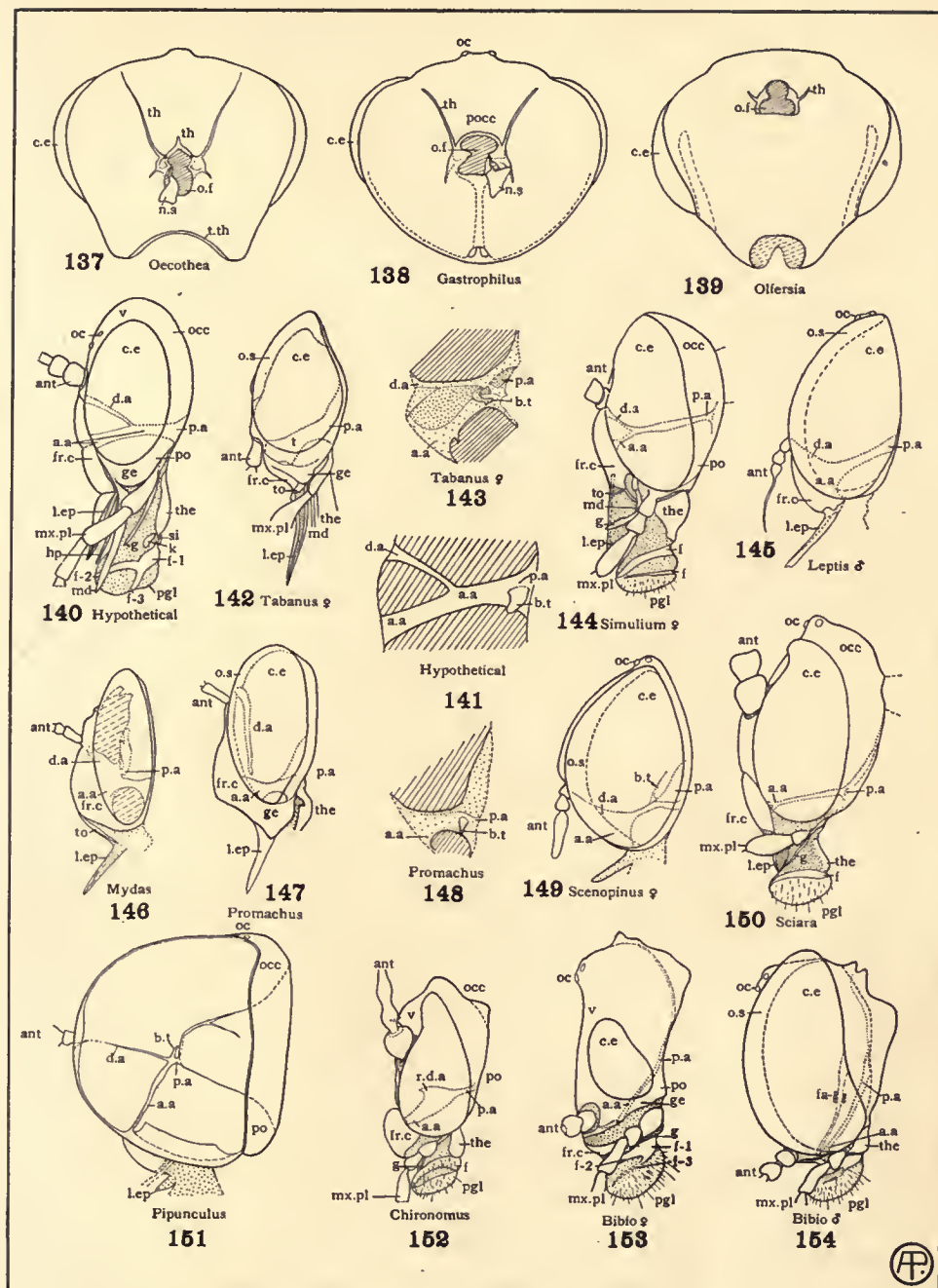




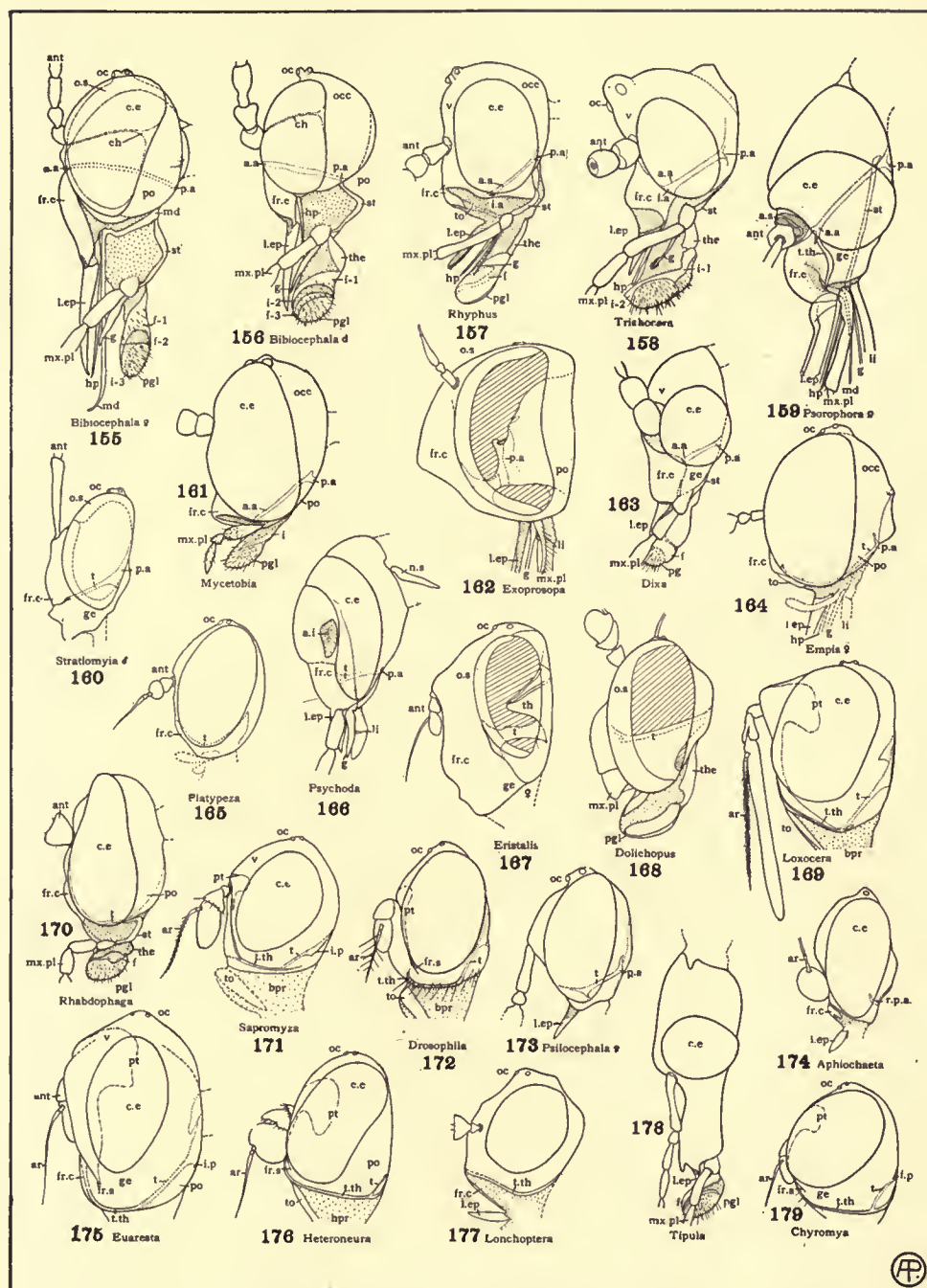


PLATE IX

## EXPLANATION OF PLATE

## LATERAL ASPECT OF THE HEAD SHOWING THE TENTORIUM

- Fig. 155. *Bibliocephala elegantula*, female.
- Fig. 156. *Bibliocephala elegantula*, male.
- Fig. 157. *Rhyphus punctatus*.
- Fig. 158. *Trichocera bimacula*.
- Fig. 159. *Psorophora ciliata*, female.
- Fig. 160. *Stratiomyia apicula*, male.
- Fig. 161. *Mycetobia divergens*.
- Fig. 162. *Exoprosopa fasciata*, eye removed.
- Fig. 163. *Dixa clavata*.
- Fig. 164. *Empis clausa*, female.
- Fig. 165. *Platypeza velutina*.
- Fig. 166. *Psychoda albipennis*.
- Fig. 167. *Eristalis tenax*, female, eye removed.
- Fig. 168. *Dolichopus bifractus*, eye removed.
- Fig. 169. *Loxocera pectoralis*.
- Fig. 170. *Rhabdophaga strobiloides*.
- Fig. 171. *Sapromyza vulgaris*.
- Fig. 172. *Drosophila ampelophila*.
- Fig. 173. *Psilocephala haemorrhoidalis*, female.
- Fig. 174. *Aphiochaeta agarici*.
- Fig. 175. *Euaresta aequalis*.
- Fig. 176. *Heteroneura flaviseta*.
- Fig. 177. *Lonchoptera lutea*.
- Fig. 178. *Tipula bicornis*.
- Fig. 179. *Chyromya concolor*.





## PLATE X



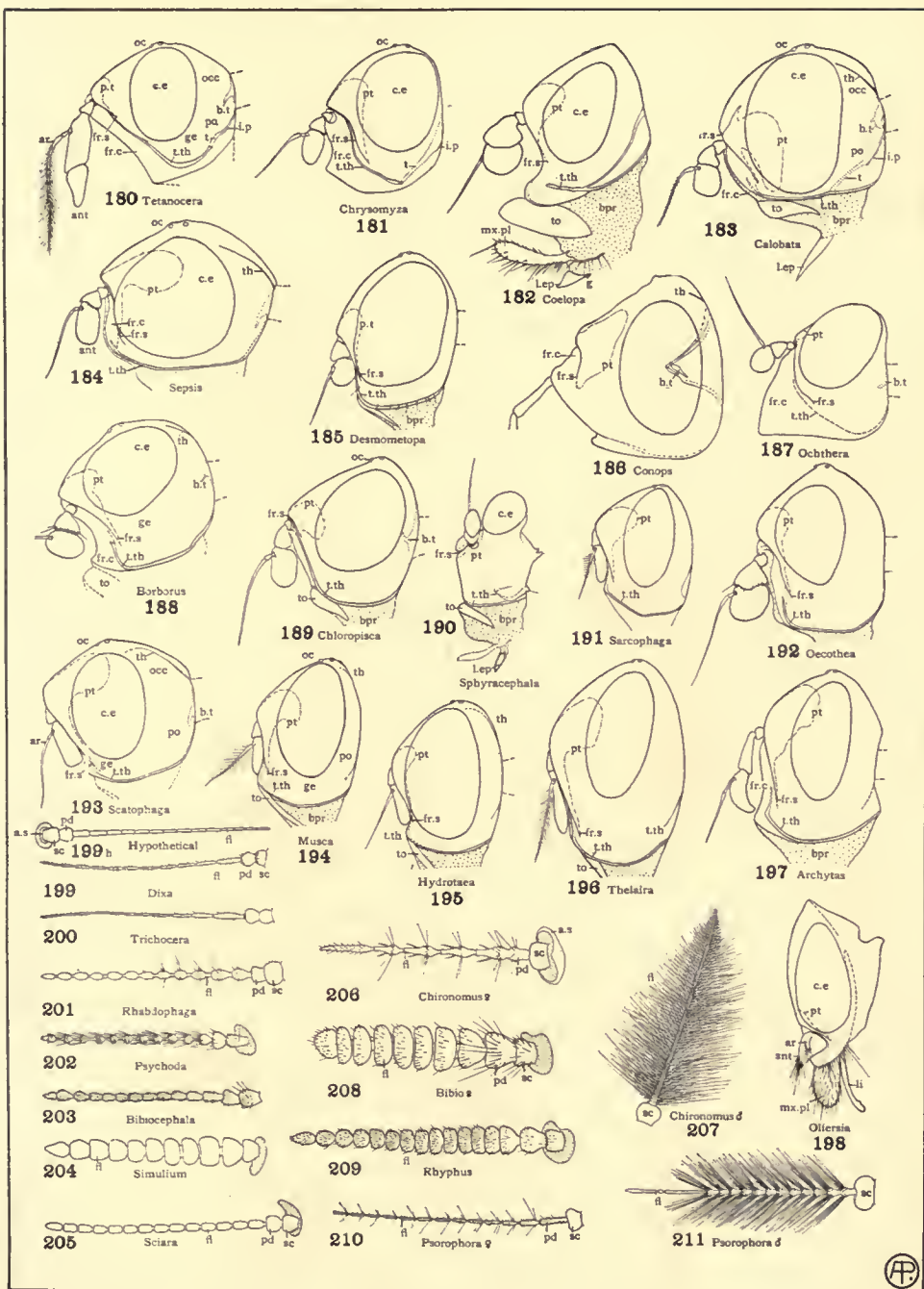
## EXPLANATION OF PLATE

## LATERAL ASPECT OF THE HEAD SHOWING THE TENTORIUM

- |  |   |
|--|---|
| Fig. 180. <i>Tetanocera plumosa</i> .    | Fig. 190. <i>Sphyracephala brevicornis</i> .  |
| Fig. 181. <i>Chrysomya demandata</i> .   | Fig. 191. <i>Sarcophaga haemorrhoidalis</i> . |
| Fig. 182. <i>Coelopa vanduzeei</i> .     | Fig. 192. <i>Oeciothea fenestralis</i> .      |
| Fig. 183. <i>Calobata univitta</i> .     | Fig. 193. <i>Scatophaga furcata</i> .         |
| Fig. 184. <i>Sepsis violacea</i> .       | Fig. 194. <i>Musca domestica</i> .            |
| Fig. 185. <i>Desmometopa latipes</i> .   | Fig. 195. <i>Hydrotaea dentipes</i> .         |
| Fig. 186. <i>Conops brachyrhynchus</i> . | Fig. 196. <i>Thelaira leucozona</i> .         |
| Fig. 187. <i>Ochthera mantis</i> .       | Fig. 197. <i>Archytas analis</i> .            |
| Fig. 188. <i>Borborus equinus</i> .      | Fig. 198. <i>Olfersia ardeae</i> .            |
| Fig. 189. <i>Chloropisca glabra</i> .    |   |

## ANTENNAE

- |   |  |
|---|--|
| Fig. 199h. Hypothetical antenna.            | Fig. 206. <i>Chironomus ferrugineovittatus</i> , female. |
| Fig. 199. <i>Dixa clavata</i> .             | Fig. 207. <i>Chironomus ferrugineovittatus</i> , male.   |
| Fig. 200. <i>Trichocera bimacula</i> .      | Fig. 208. <i>Bibio femoratus</i> , female.               |
| Fig. 201. <i>Rhabdophaga strobiloides</i> . | Fig. 209. <i>Rhyphus punctatus</i> .                     |
| Fig. 202. <i>Psychoda albipennis</i> .      | Fig. 210. <i>Psorophora ciliata</i> , female.            |
| Fig. 203. <i>Bibiocephala elegantula</i> .  | Fig. 211. <i>Psorophora ciliata</i> , male.              |
| Fig. 204. <i>Simulium venustum</i> .        |  |
| Fig. 205. <i>Sciara varians</i> .           |  |





## PLATE XI

## EXPLANATION OF PLATE

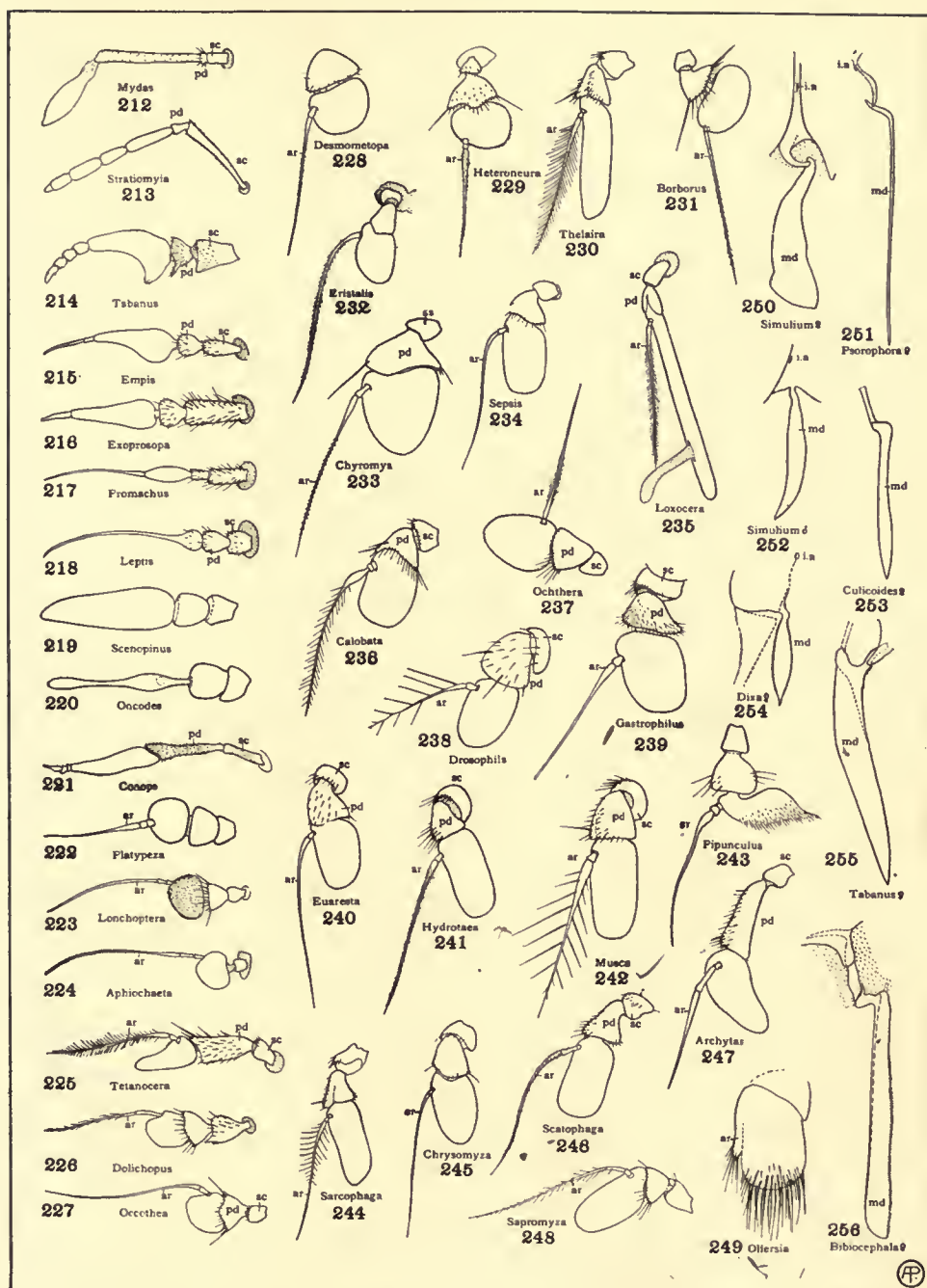
## ANTENNAE

- |   |   |
|---|---|
| Fig. 212. <i>Mydas clavatus</i> .         | Fig. 231. <i>Borborus equinus</i> .           |
| Fig. 213. <i>Stratiomyia apicula</i> .    | Fig. 232. <i>Eristalis tenax</i> .            |
| Fig. 214. <i>Tabanus giganteus</i> .      | Fig. 233. <i>Chyromya concolor</i> .          |
| Fig. 215. <i>Empis clausa</i> .           | Fig. 234. <i>Sepsis violacea</i> .            |
| Fig. 216. <i>Exoprosopa fasciata</i> .    | Fig. 235. <i>Loxocera pectoralis</i> .        |
| Fig. 217. <i>Promachus vertebratus</i> .  | Fig. 236. <i>Calobata univitta</i> .          |
| Fig. 218. <i>Leptis vertebrata</i> .      | Fig. 237. <i>Ochthera mantis</i> .            |
| Fig. 219. <i>Scenopinus fenestralis</i> . | Fig. 238. <i>Drosophila ampelophila</i> .     |
| Fig. 220. <i>Oncodes costatus</i> .       | Fig. 239. <i>Gastrophilus equi</i> .          |
| Fig. 221. <i>Conops brachyrhynchus</i> .  | Fig. 240. <i>Euaresta aequalis</i> .          |
| Fig. 222. <i>Platypeza velutina</i> .     | Fig. 241. <i>Hydrotaea dentipes</i> .         |
| Fig. 223. <i>Lonchoptera lutea</i> .      | Fig. 242. <i>Musca domestica</i> .            |
| Fig. 224. <i>Aphiochaeta agarici</i> .    | Fig. 243. <i>Pipunculus cingulatus</i> .      |
| Fig. 225. <i>Tetanocera plumosa</i> .     | Fig. 244. <i>Sarcophaga haemorrhoidalis</i> . |
| Fig. 226. <i>Dolichopus bifraetus</i> .   | Fig. 245. <i>Chrysomya demandata</i> .        |
| Fig. 227. <i>Oeciothea fenestralis</i> .  | Fig. 246. <i>Scatophaga furcata</i> .         |
| Fig. 228. <i>Desmometopa latipes</i> .    | Fig. 247. <i>Archytas analis</i> .            |
| Fig. 229. <i>Heteroneura flaviseta</i> .  | Fig. 248. <i>Sapromyza vulgaris</i> .         |
| Fig. 230. <i>Thelaira leucozona</i> .     | Fig. 249. <i>Olfersia ardeae</i> .            |

## MANDIBLES

- |   |  |
|---|--|
| Fig. 250. <i>Simulium venustum</i> , female.      | Fig. 254. <i>Dixa modesta</i> , female.            |
| Fig. 251. <i>Psorophora ciliata</i> , female.     | Fig. 255. <i>Tabanus giganteus</i> , female.       |
| Fig. 252. <i>Simulium johannseni</i> , male.      | Fig. 256. <i>Bibiocephala elegantula</i> , female. |
| Fig. 253. <i>Culicoides sanguisugus</i> , female. |  |





PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XI

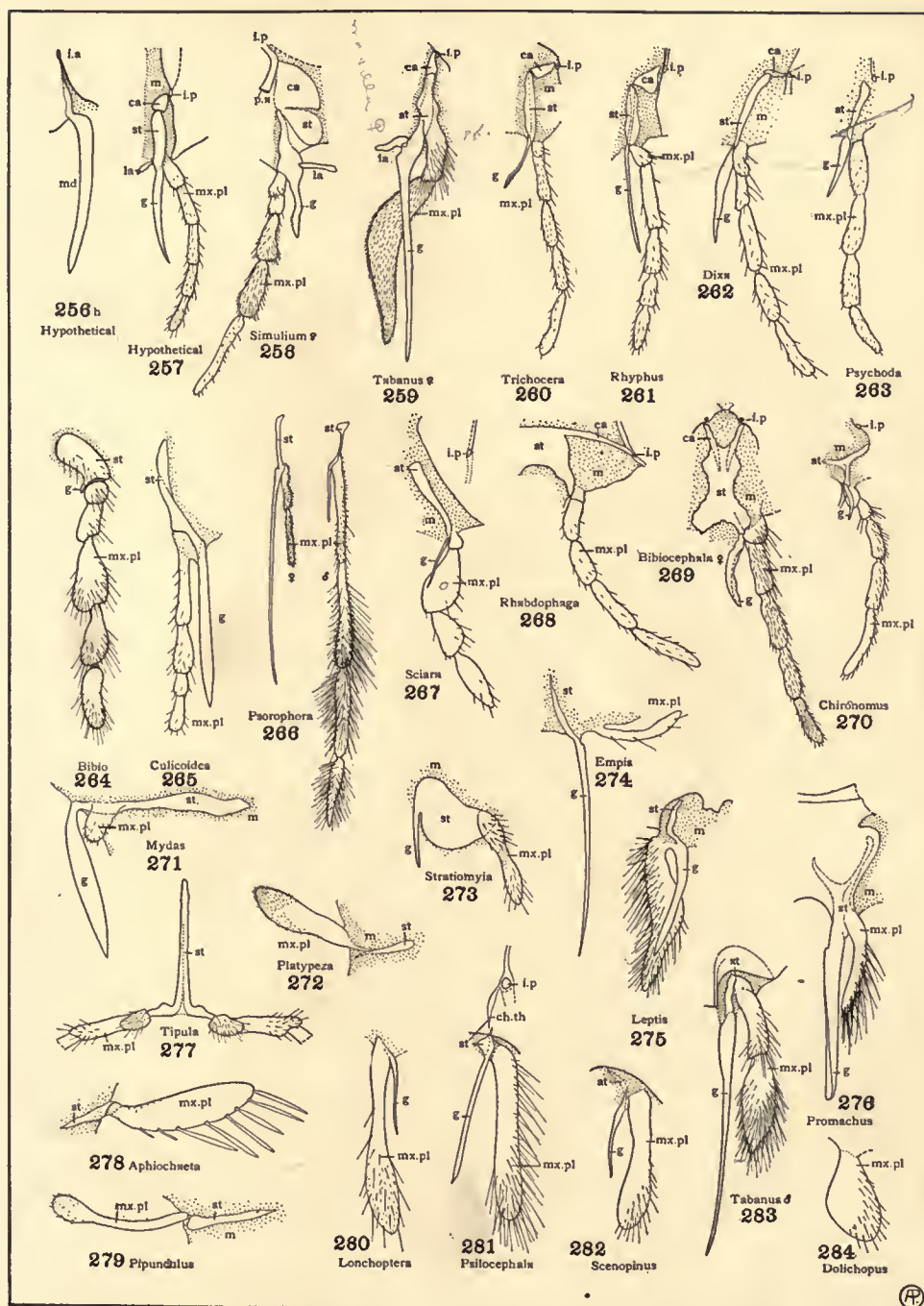


## PLATE XII

## EXPLANATION OF PLATE

## MANDIBLE AND MAXILLAE

- Fig. 256h. Hypothetical mandible.  
Fig. 257. Hypothetical maxillae.  
Fig. 258. *Simulium venustum*, female, cephalic aspect.  
Fig. 259. *Tabanus giganteus*, female, caudal aspect.  
Fig. 260. *Trichocera bimacula*, caudal aspect.  
Fig. 261. *Rhyphus punctatus*, caudal aspect.  
Fig. 262. *Dixa clavata*, caudal aspect.  
Fig. 263. *Psychoda albipennis*, caudal aspect.  
Fig. 264. *Bibio femoratus*, caudal aspect.  
Fig. 265. *Culicoides sanguisugus*, female, caudal aspect.  
Fig. 266. *Psorophora ciliata*, female and male, caudal aspect.  
Fig. 267. *Sciara varians*, caudal aspect.  
Fig. 268. *Rhabdophaga strobiloides*, caudal aspect.  
Fig. 269. *Bibiocephala elegantula*, female, caudal aspect.  
Fig. 270. *Chironomus ferrugineovittatus*, cephalic aspect.  
Fig. 271. *Mydas clavatus*, lateral aspect.  
Fig. 272. *Platypeza velutina*, lateral aspect.  
Fig. 273. *Stratiomyia apicula*, cephalic aspect.  
Fig. 274. *Empis clausa*, lateral aspect.  
Fig. 275. *Leptis vertebrata*, caudal aspect.  
Fig. 276. *Promachus vertebratus*, caudal aspect.  
Fig. 277. *Tipula bicornis*, portion of caudal aspect.  
Fig. 278. *Aphiochaeta agarici*, lateral aspect.  
Fig. 279. *Pipunculus cingulatus*, lateral aspect.  
Fig. 280. *Lonchoptera lutea*.  
Fig. 281. *Psilocephala haemorrhoidalis*, cephalic aspect.  
Fig. 282. *Scenopinus fenestralis*.  
Fig. 283. *Tabanus giganteus*, male, caudal aspect.  
Fig. 284. *Dolichopus bifractus*.





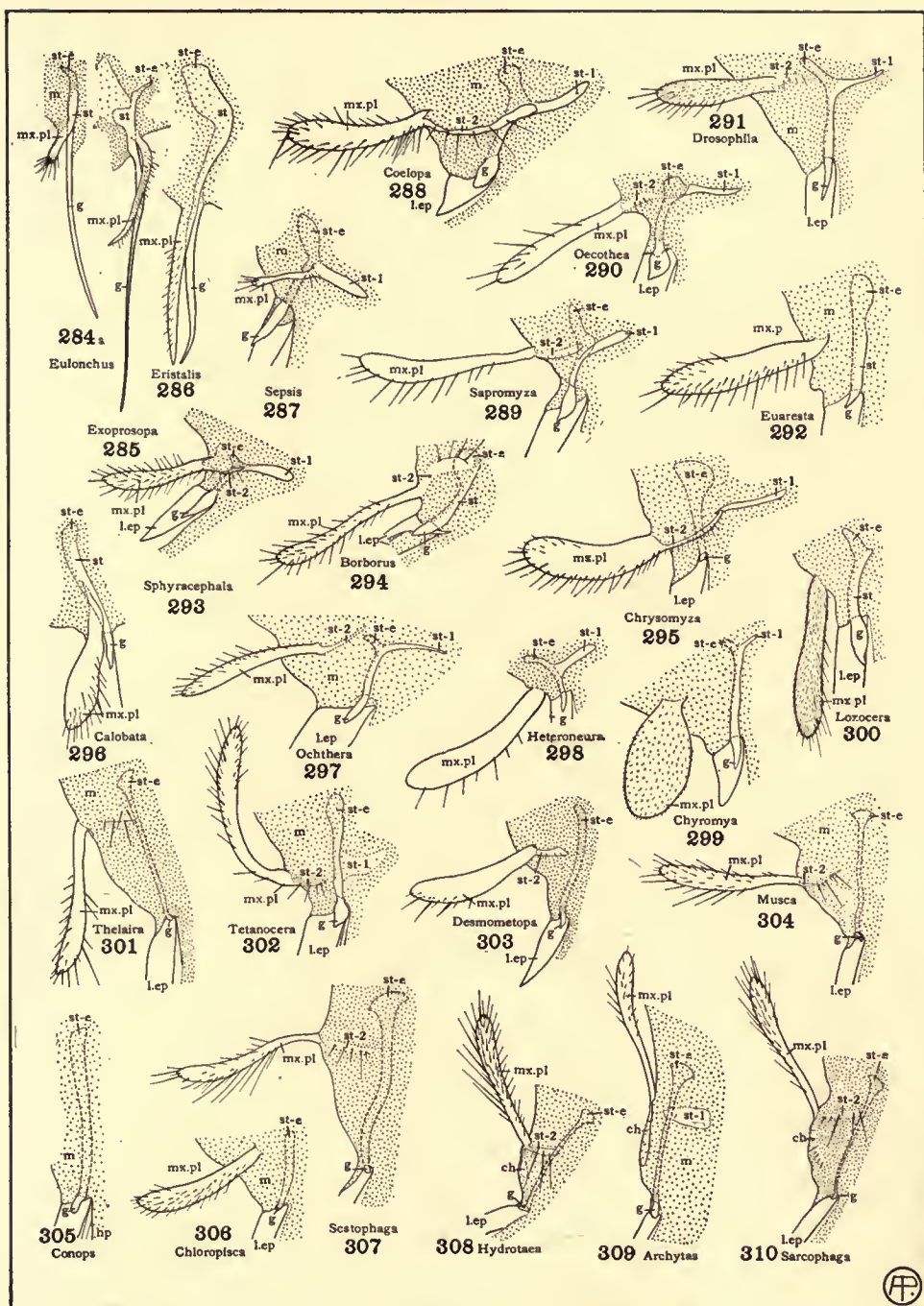


## PLATE XIII

## EXPLANATION OF PLATE

## MAXILLAE

- Fig. 284a. *Eulonchus tristis*.  
Fig. 285. *Exoprosopa fasciata*.  
Fig. 286. *Eristalis tenax*.  
Fig. 287. *Sepsis violacea*.  
Fig. 288. *Coelopa vanduzeei*.  
Fig. 289. *Sapromyza vulgaris*.  
Fig. 290. *Oecothoa fenestralis*.  
Fig. 291. *Drosophila ampelophila*.  
Fig. 292. *Euaresta aequalis*.  
Fig. 293. *Sphyracephala brevicornis*.  
Fig. 294. *Borborus equinus*.  
Fig. 295. *Chrysomya demandata*.  
Fig. 296. *Calobata univitta*.  
Fig. 297. *Ochthera mantis*.  
Fig. 298. *Heteroneura flaviseta*.  
Fig. 299. *Chyromya concolor*.  
Fig. 300. *Loxocera pectoralis*.  
Fig. 301. *Thelaira leucozona*.  
Fig. 302. *Tetanocera plumosa*.  
Fig. 303. *Desmometopa latipes*.  
Fig. 304. *Musca domestica*.  
Fig. 305. *Conops brachyrhynchus*.  
Fig. 306. *Chloropisca glabra*.  
Fig. 307. *Scatophaga furcata*.  
Fig. 308. *Hydrotaea dentipes*.  
Fig. 309. *Archytos analis*.  
Fig. 310. *Sarcophaga haemorrhoidalis*.



PETERSON HEAD AND MOUTH PARTS OF DIPTERA PLATE XIII



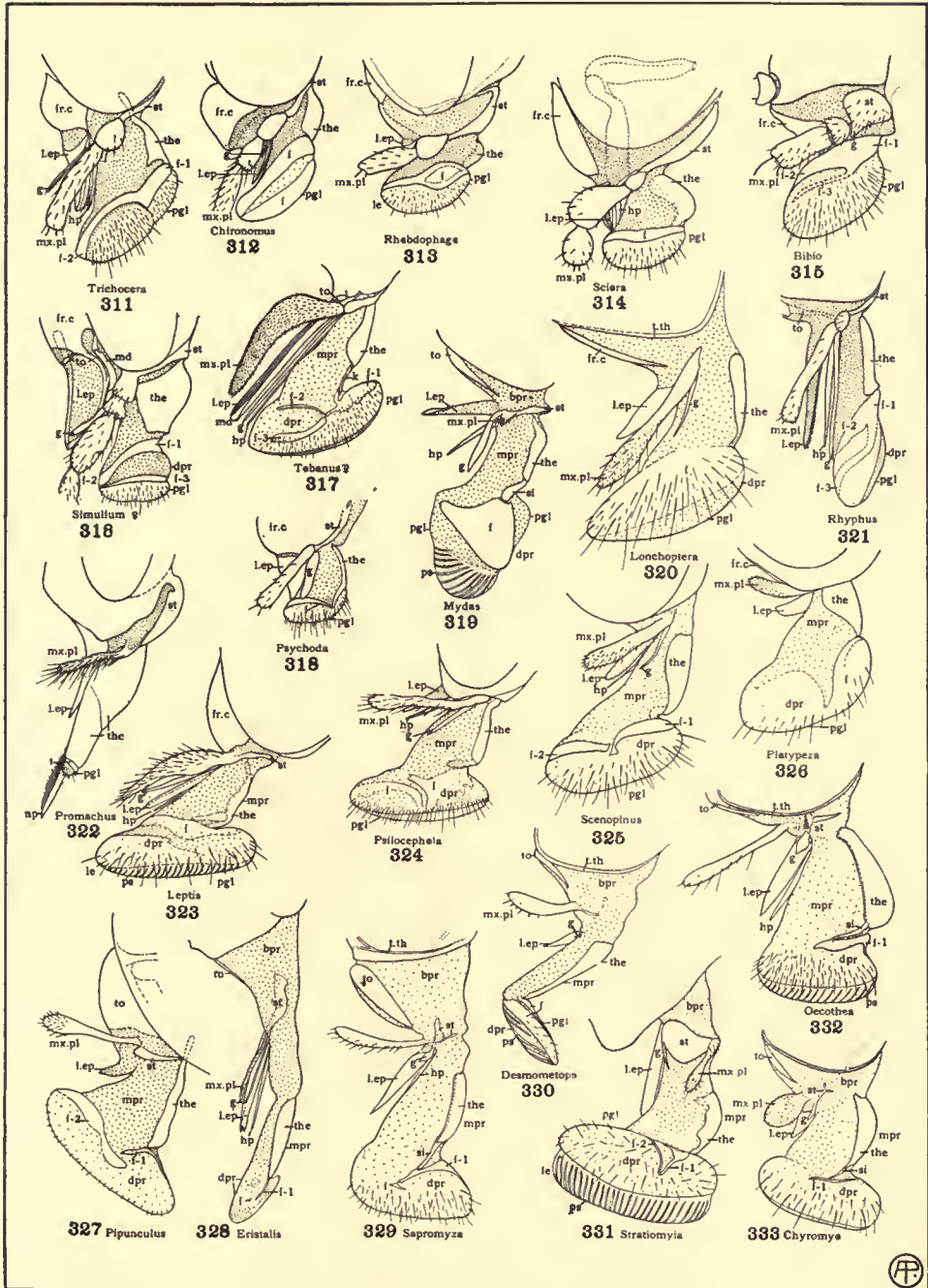


## PLATE XIV

## EXPLANATION OF PLATE

## LATERAL ASPECT OF THE MOUTH-PARTS OR PROBOSCIS

- Fig. 311. *Trichocera bimacula*.
- Fig. 312. *Chironomus ferrugineovittatus*.
- Fig. 313. *Rhabdophaga strobiloides*.
- Fig. 314. *Sciarà varians*.
- Fig. 315. *Bibio femoratus*.
- Fig. 316. *Simulium venustum*, female.
- Fig. 317. *Tabanus giganteus*, female.
- Fig. 318. *Psychoda albipennis*.
- Fig. 319. *Mydas clavatus*.
- Fig. 320. *Lonchoptera lutea*.
- Fig. 321. *Rhyphus punctatus*.
- Fig. 322. *Promachus vertebratus*.
- Fig. 323. *Leptis vertebrata*.
- Fig. 324. *Psilocephala haemorrhoidalis*.
- Fig. 325. *Scenopinus fenestralis*.
- Fig. 326. *Platypeza velutina*.
- Fig. 327. *Pipunculus cingulatus*.
- Fig. 328. *Eristalis tenax*.
- Fig. 329. *Sapromyza vulgaris*.
- Fig. 330. *Desmometopa latipes*.
- Fig. 331. *Stratiomyia apicula*.
- Fig. 332. *Oecotha fenestralis*.
- Fig. 333. *Chyromyza concolor*.





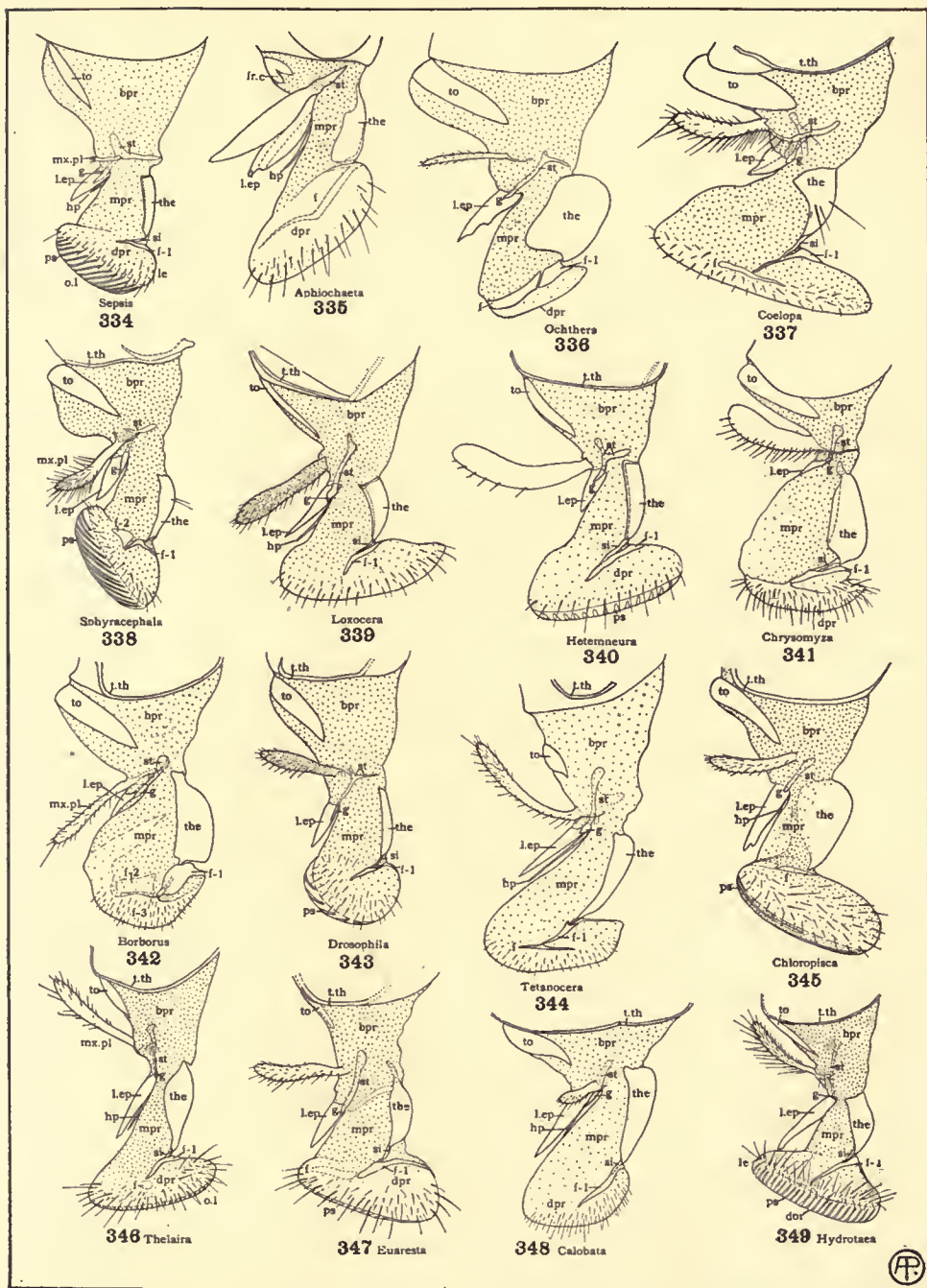
## PLATE XV



## EXPLANATION OF PLATE

## LATERAL ASPECT OF THE PROBOSCIS

- Fig. 334. *Sepsis violacea*.  
Fig. 335. *Aphiochaeta agarici*.  
Fig. 336. *Ochthera mantis*.  
Fig. 337. *Coelopa vanduzeei*.  
Fig. 338. *Sphyracephala brevicornis*.  
Fig. 339. *Loxocera pectoralis*.  
Fig. 340. *Heteroneura flaviseta*.  
Fig. 341. *Chrysomya demandata*.  
Fig. 342. *Barbarus equinus*.  
Fig. 343. *Drosophila ampelophila*.  
Fig. 344. *Tetanocera plumosa*.  
Fig. 345. *Chloropisca glabra*.  
Fig. 346. *Thelaira leucozona*.  
Fig. 347. *Euaresta aequalis*.  
Fig. 348. *Calobata univitta*.  
Fig. 349. *Hydrotaea dentipes*.





## PLATE XVI

## EXPLANATION OF PLATE

## MOUTH-PARTS

- Fig. 350. *Sarcophaga haemorrhoidalis*, lateral aspect.  
✓ Fig. 351. *Musca domestica*, lateral aspect.  
Fig. 352. *Empis clausa*, lateral aspect.  
Fig. 353. *Archytas analis*, lateral aspect.  
Fig. 354. *Stomoxys calcitrans*, lateral aspect.  
Fig. 355. *Siphona geniculata*, lateral aspect.  
Fig. 356. *Conops brachyrhynchus*, lateral aspect.  
Fig. 357. *Scatophaga furcata*, lateral aspect.  
Fig. 358. *Olfersia ardcae*, lateral aspect.  
Fig. 359. *Stylogaster biannulata*, caudal aspect.  
Fig. 360. *Sciara varians*, maxillae and labium, cephalic aspect.  
Fig. 361. *Exoprosopa fasciata*, lateral aspect.  
Fig. 362. Hypothetical and typical labium, mesal aspect.  
Fig. 363. Hypothetical mouth-parts, lateral aspect.  
Fig. 364. *Bibio femoratus*, maxillae and labium, cephalic aspect.  
Fig. 364a. *Eulonchus tristis*, head and mouth-parts, lateral aspect.  
Fig. 365. *Trichocera bimacula*, maxillae and labium, cephalic aspect.  
Fig. 366. *Simulium venustum*, maxillae and labium, cephalic aspect.  
Fig. 367. *Rhabdophaga strobiloides*, maxillae and labium, caudal aspect.  
Fig. 368. *Leia oblectabilis*, maxillae and labium, cephalic aspect.  
Fig. 369. *Leptis vertebrata*, mesal aspect of glossa.  
Fig. 370. *Leptis vertebrata*, maxillae and labium, caudal aspect.





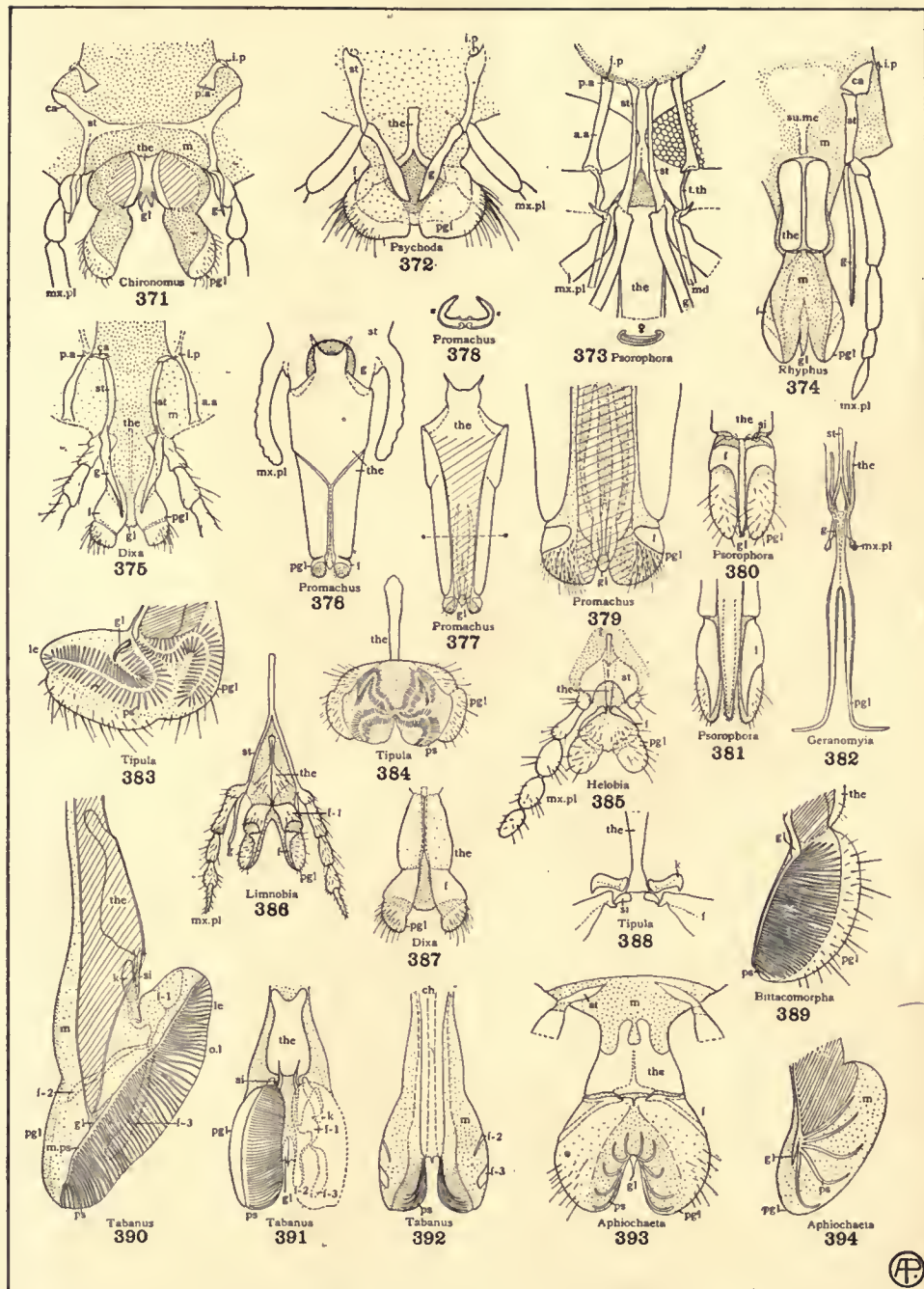


## PLATE XVII

## EXPLANATION OF PLATE

## MAXILLAE AND LABIUM

- Fig. 371. *Chironomus ferrugineovittatus*, cephalic aspect.  
Fig. 372. *Psychoda albipennis*, cephalic aspect.  
Fig. 373. *Psorophora ciliata*, female, portions of mandibles, maxillae, labium, tentorium, and head-capsule.  
Fig. 374. *Rhyphus punctatus*, cephalic aspect.  
Fig. 375. *Dixa clavata*, cephalic aspect.  
Fig. 376. *Promachus vertebratus*, caudal aspect.  
Fig. 377. *Promachus vertebratus*, labium, cephalic aspect.  
Fig. 378. *Promachus vertebratus*, cross-section of labium, see figure 377.  
Fig. 379. *Promachus vertebratus*, distal end of labium, cephalic aspect.  
Fig. 380. *Psorophora ciliata*, distal end of labium, caudal aspect.  
Fig. 381. *Psorophora ciliata*, distal end of labium, cephalic aspect.  
Fig. 382. *Geranomyia canadensis*, cephalic aspect.  
Fig. 383. *Tipula bicornis*, distal end of labium, mesal aspect.  
Fig. 384. *Tipula bicornis*, caudal aspect of labium.  
Fig. 385. *Helobia punctipennis*, caudal aspect.  
Fig. 386. *Limnobia immatura*, caudal aspect.  
Fig. 387. *Dixa clavata*, caudal aspect of labium.  
Fig. 388. *Tipula bicornis*, sclerites about distal end of theca of labium.  
Fig. 389. *Bittacomorpha clavipes*, distal end of labium, mesal aspect.  
Fig. 390. *Tabanus giganteus*, mesal aspect of labium.  
Fig. 391. *Tabanus giganteus*, caudal aspect of labium.  
Fig. 392. *Tabanus giganteus*, cephalic aspect of labium.  
Fig. 393. *Aphiochaeta agarici*, caudal aspect.  
Fig. 394. *Aphiochaeta agarici*, distal end of labium, mesal aspect.







## PLATE XVIII

## EXPLANATION OF PLATE

## LABIUM

- Fig. 395. *Stratiomyia apicula*, caudal aspect of proboscis.  
 Fig. 396. *Stratiomyia apicula*, mesal aspect.  
 Fig. 397. *Mydas clavatus*, caudal aspect.  
 Fig. 398. *Mydas clavatus*, cephalic aspect.  
 Fig. 399. *Bibiocephala elegantula*, cephalic aspect.  
 Fig. 400. *Scenopinus fenestralis*, mesal aspect.  
 Fig. 401. *Scenopinus fenestralis*, caudal aspect.  
 Fig. 402. *Psilocephala haemorrhoidalis*, caudal aspect.  
 Fig. 403. *Psilocephala haemorrhoidalis*, mesal aspect.  
 Fig. 404. *Desmometopa latipes*, caudal aspect.  
 Fig. 405. *Desmometopa latipes*, cephalic aspect.  
 Fig. 406. *Lonchoptera lutea*, caudal aspect.  
 Fig. 407. *Lonchoptera lutea*, cephalic aspect.  
 Fig. 408. *Lonchoptera lutea*, mesal aspect.  
 Fig. 409. *Sapromyza vulgaris*, caudal aspect.  
 Fig. 410. *Sapromyza vulgaris*, mesal aspect.  
 Fig. 411. *Chyromyia concolor*, caudal aspect.  
 Fig. 412. *Chyromyia concolor*, mesal aspect.  
 Fig. 413. *Euaresta aequalis*, caudal aspect.  
 Fig. 414. *Euaresta aequalis*, mesal aspect.  
 Fig. 415. *Platypeza velutina*, mesal aspect.  
 Fig. 416. *Platypeza velutina*, caudal aspect.  
 Fig. 417. *Conops brachyrhynchus*, distal end, caudal aspect.  
 Fig. 418. *Conops brachyrhynchus*, distal end, lateral aspect.  
 Fig. 419. *Conops brachyrhynchus*, distal end, cephalic aspect.  
 Fig. 420. *Conops brachyrhynchus*, caudal aspect.  
 Fig. 421. *Empis clausa*, caudal aspect.  
 Fig. 422. *Empis clausa*, portion of cephalic aspect.  
 Fig. 423. *Empis clausa*, cephalic aspect.  
 Fig. 424. *Rhamphomyia glabra*, caudal aspect.  
 Fig. 425. *Rhamphomyia glabra*, mesal aspect.  
 Fig. 425a. *Eulonchus tristis*, cephalic aspect.  
 Fig. 425b. *Eulonchus tristis*, distal end, mesal aspect.  
 Fig. 426. *Exoprosopa fasciata*, distal end, caudal aspect.  
 Fig. 427. *Exoprosopa fasciata*, cephalic aspect.  
 Fig. 428. *Exoprosopa fasciata*, distal end, mesal aspect.  
 Fig. 429. *Exoprosopa fasciata*, caudal aspect.

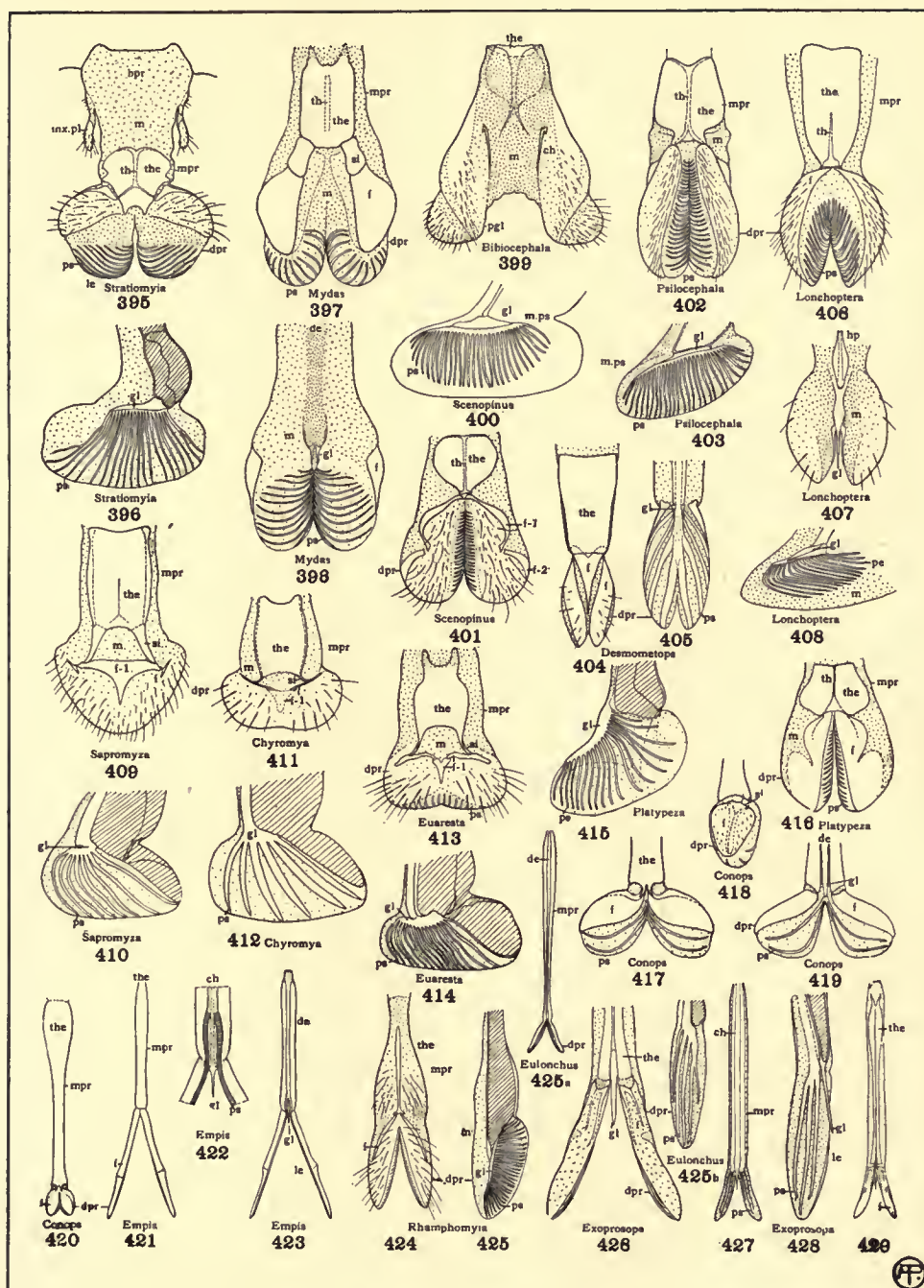




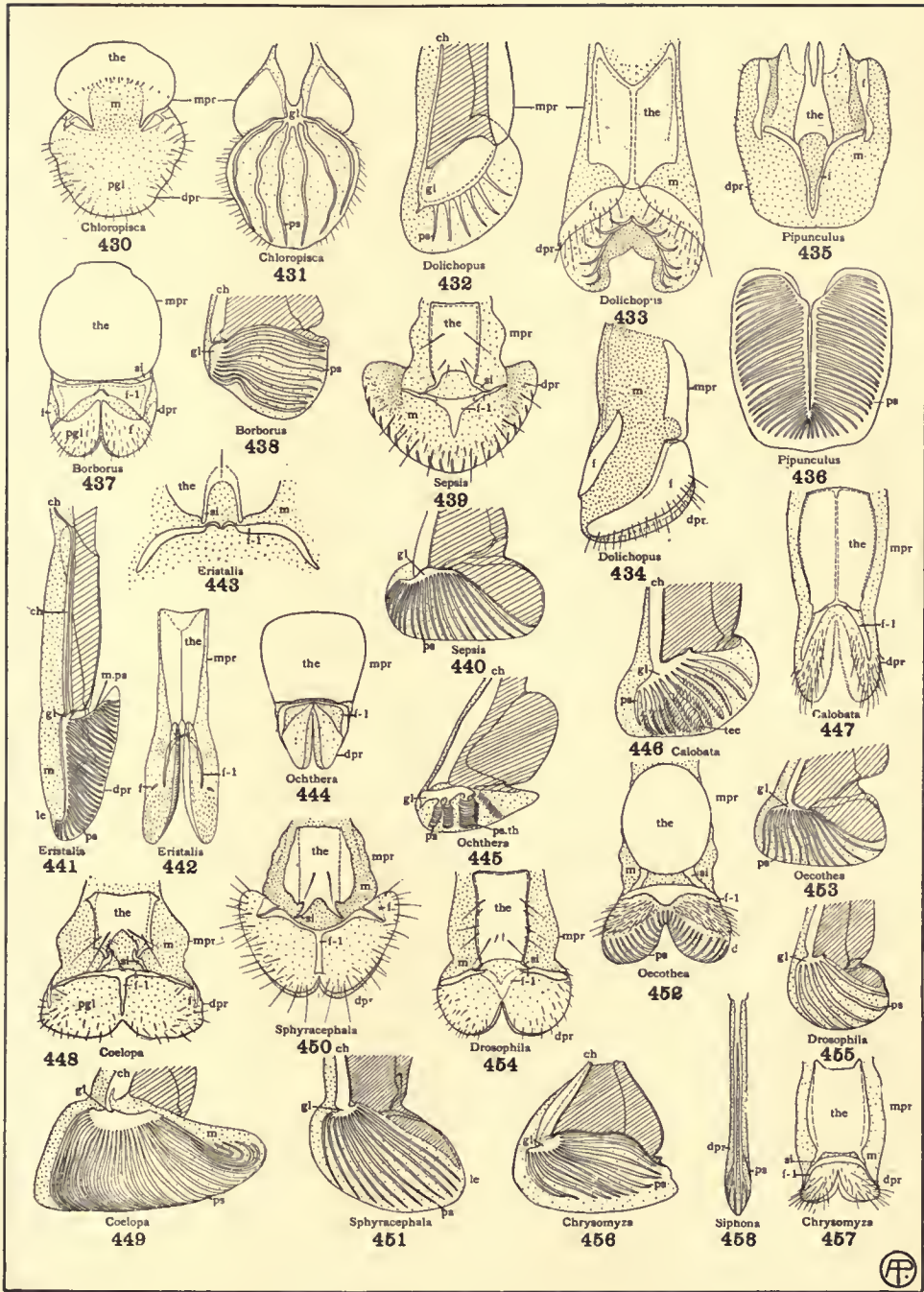


PLATE XIX

## EXPLANATION OF PLATE

## LABIUM

- Fig. 430. *Chloropisca glabra*, caudal aspect.  
Fig. 431. *Chloropisca glabra*, cephalic aspect.  
Fig. 432. *Dolichopus bifractus*, mesal aspect.  
Fig. 433. *Dolichopus bifractus*, caudal aspect.  
Fig. 434. *Dolichopus bifractus*, lateral aspect.  
Fig. 435. *Pipunculus cingulatus*, caudal aspect.  
Fig. 436. *Pipunculus cingulatus*, cephalic aspect.  
Fig. 437. *Borborus equinus*, caudal aspect.  
Fig. 438. *Borborus equinus*, mesal aspect.  
Fig. 439. *Sepsis violacea*, caudal aspect.  
Fig. 440. *Sepsis violacea*, mesal aspect.  
Fig. 441. *Eristalis tenax*, mesal aspect.  
Fig. 442. *Eristalis tenax*, caudal view.  
Fig. 443. *Eristalis tenax*, distal end of theca, caudal aspect.  
Fig. 444. *Ochthera mantis*, caudal aspect.  
Fig. 445. *Ochthera mantis*, mesal aspect.  
Fig. 446. *Calobata univitta*, mesal aspect.  
Fig. 447. *Calobata univitta*, caudal aspect.  
Fig. 448. *Coelopa vanduzeei*, caudal aspect.  
Fig. 449. *Coelopa vanduzeei*, mesal aspect.  
Fig. 450. *Sphyracephala brevicornis*, caudal aspect.  
Fig. 451. *Sphyracephala brevicornis*, mesal aspect.  
Fig. 452. *Oecotheca fenestralis*, caudal aspect.  
Fig. 453. *Oecotheca fenestralis*, mesal aspect.  
Fig. 454. *Drosophila ampelophila*, caudal aspect.  
Fig. 455. *Drosophila ampelophila*, mesal aspect.  
Fig. 456. *Chrysomya demandata*, mesal aspect.  
Fig. 457. *Chrysomya demandata*, caudal aspect.  
Fig. 458. *Siphona geniculata*, distal end, cephalic aspect.





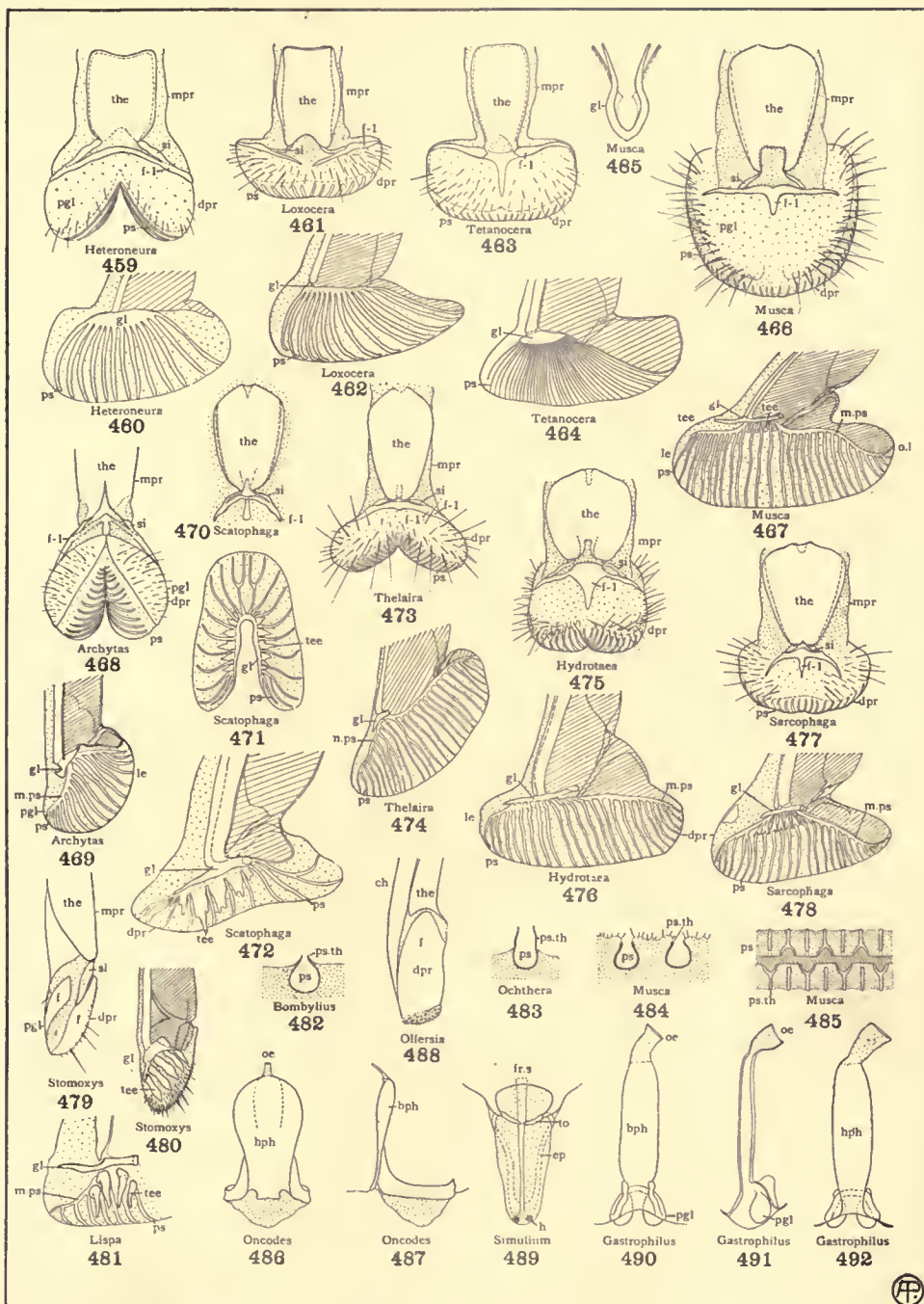
## PLATE XX



## EXPLANATION OF PLATE

## LABIUM AND OTHER PARTS

- Fig. 459. *Heteroneura flaviseta*, caudal aspect.
- Fig. 460. *Heteroneura flaviseta*, mesal aspect.
- Fig. 461. *Loxocera pectoralis*, caudal aspect.
- Fig. 462. *Loxocera pectoralis*, mesal aspect.
- Fig. 463. *Tetanocera plumosa*, caudal aspect.
- Fig. 464. *Tetanocera plumosa*, mesal aspect.
- ✓ Fig. 465. *Musca domestica*, dorsal aspect of glossae.
- Fig. 466. *Musca domestica*, caudal aspect.
- Fig. 467. *Musca domestica*, mesal aspect.
- Fig. 468. *Archytas analis*, caudal aspect.
- Fig. 469. *Archytas analis*, mesal aspect.
- Fig. 470. *Scatophaga furcata*, caudal aspect of mediproboscis.
- Fig. 471. *Scatophaga furcata*, ventral aspect of distiproboscis.
- Fig. 472. *Scatophaga furcata*, mesal aspect.
- Fig. 473. *Thelaira leucozona*, caudal aspect.
- Fig. 474. *Thelaira leucozona*, mesal aspect.
- Fig. 475. *Hydrotaea dentipes*, caudal aspect.
- Fig. 476. *Hydrotaea dentipes*, mesal aspect.
- Fig. 477. *Sarcophaga haemorrhoidalis*, caudal aspect.
- Fig. 478. *Sarcophaga haemorrhoidalis*, mesal aspect.
- Fig. 479. *Stomoxys calcitrans*, distal end, lateral aspect.
- Fig. 480. *Stomoxys calcitrans*, distal end, mesal aspect.
- Fig. 481. *Lispa nasoni*, distal end, mesal aspect.
- Fig. 482. *Bombylius major*, cross-section thru pseudotrachea. (After Dimmock.)
- Fig. 483. *Ochthera mantis*, cross-section thru pseudotrachea.
- Fig. 484. *Musca (Calliphora) vomitoria*, cross-section thru pseudotrachea (After Dimmock.)
- Fig. 485. *Musca (Calliphora) vomitoria*, an enlarged pseudotrachea. (After Dimmock.)
- Fig. 486. *Oncodes costatus*, entire mouth-parts, caudal aspect.
- Fig. 487. *Oncodes costatus*, entire mouth-parts, lateral aspect.
- Fig. 488. *Olfersia ordeae*, distal end, lateral aspect.
- Fig. 489. *Simulium venustum*, cephalic aspect of the labrum.
- Fig. 490. *Gastrophilus equi*, entire mouth-parts, caudal aspect.
- Fig. 491. *Gastrophilus equi*, sagittal section thru mouth-parts.
- Fig. 492. *Gastrophilus equi*, entire mouth-parts, cephalic aspect.





## PLATE XXI

## EXPLANATION OF PLATE

## EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

- Fig. 493. Hypothetical type, lateral aspect.  
Fig. 494. *Tabanus giganteus*, female, lateral aspect.  
Fig. 495. *Tabanus giganteus*, male, lateral aspect.  
Fig. 496. *Tabanus giganteus*, female, caudal aspect.  
Fig. 497. *Simulium venustum*, female, lateral aspect.  
Fig. 498. *Simulium venustum*, female, caudal aspect.  
Fig. 499. *Trichocera bimacula*, lateral aspect.  
Fig. 500. *Trichocera bimacula*, caudal aspect.  
Fig. 501. *Dixa clavata*, lateral aspect.  
Fig. 502. *Dixa clavata*, caudal aspect.  
Fig. 503. *Tipula bicornis*, lateral aspect.  
Fig. 504. *Psorophora ciliata*, female, lateral aspect.  
Fig. 505. *Psorophora ciliata*, female, caudal aspect.  
Fig. 506. *Geranomyia canadensis*, lateral aspect.  
Fig. 507. *Limnobia immatura*, lateral aspect.  
Fig. 508. *Rhyphus punctatus*, lateral aspect.  
Fig. 509. *Rhyphus punctatus*, caudal aspect.



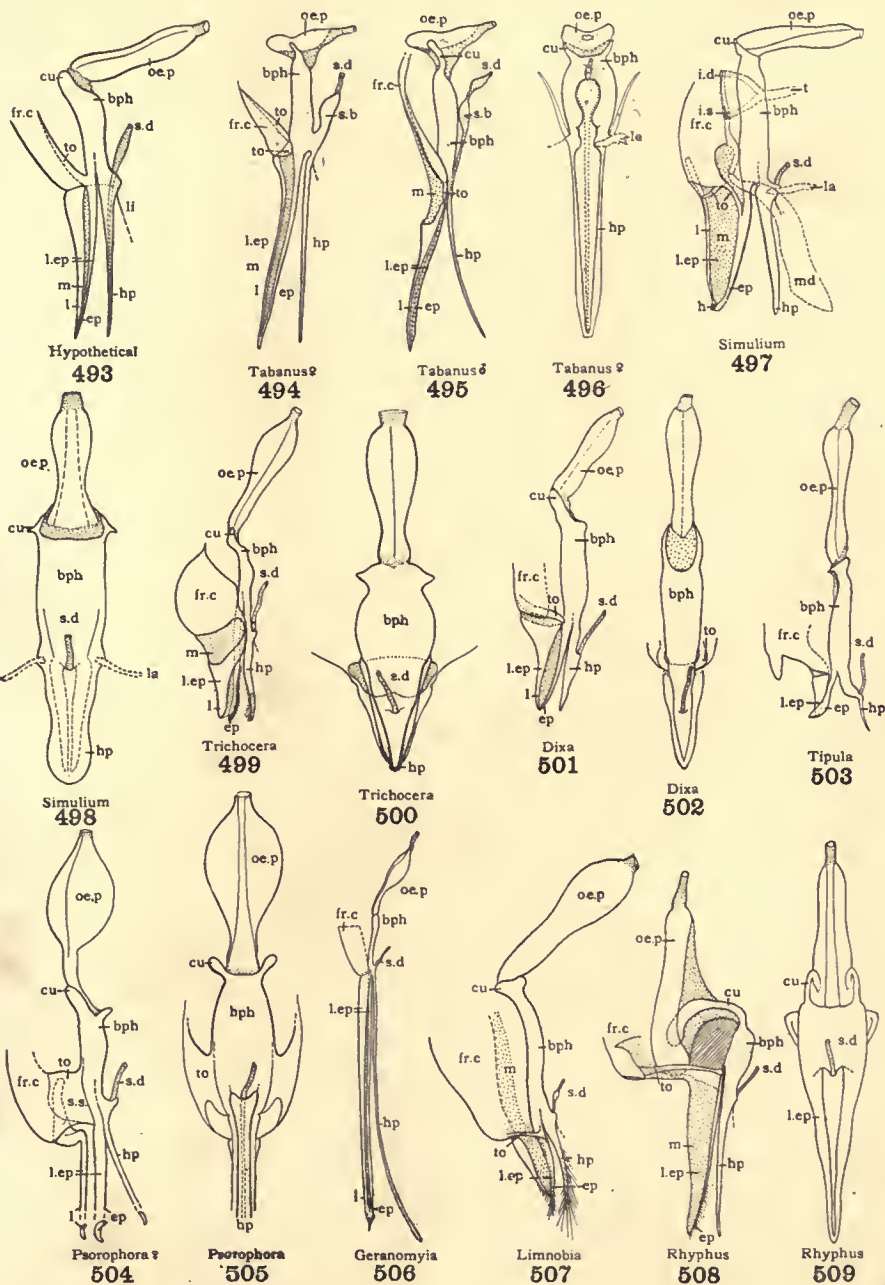


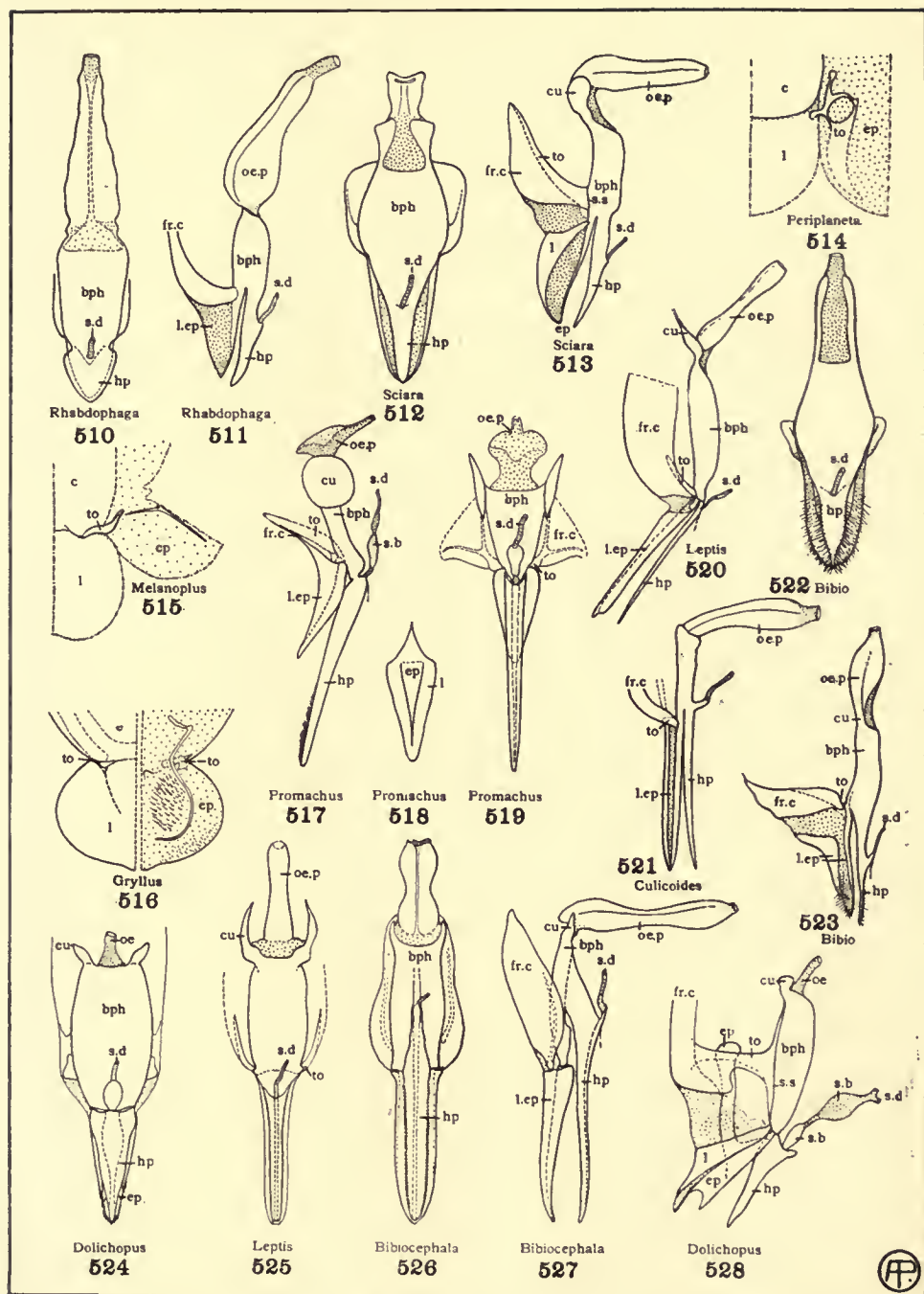


PLATE XXII

## EXPLANATION OF PLATE

## EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

- Fig. 510. *Rhabdophaga strobiloides*, caudal aspect.  
Fig. 511. *Rhabdophaga strobiloides*, lateral aspect.  
Fig. 512. *Sciara varians*, caudal aspect.  
Fig. 513. *Sciara varians*, lateral aspect.  
Fig. 514. *Periplaneta orientalis*, clypeus, labrum, and epipharynx spread out, ental aspect.  
Fig. 515. *Melanoplus differentialis*, clypeus, labrum, and epipharynx spread out, ental aspect.  
Fig. 516. *Gryllus pennsylvanicus*, right-half of clypeus, labrum, and epipharynx, cephalic and caudal aspects.  
Fig. 517. *Promachus vertebratus*, lateral aspect.  
Fig. 518. *Promachus vertebratus*, epipharynx and labrum, caudal aspect.  
Fig. 519. *Promachus vertebratus*, caudal aspect.  
Fig. 520. *Leptis vertebrata*, lateral aspect.  
Fig. 521. *Culicoides sanguisugus*, lateral aspect.  
Fig. 522. *Bibio femoratus*, caudal aspect.  
Fig. 523. *Bibio femoratus*, lateral aspect.  
Fig. 524. *Dolichopus bifractus*, caudal aspect.  
Fig. 525. *Leptis vertebrata*, caudal aspect.  
Fig. 526. *Bibiocephala elegantula*, caudal aspect.  
Fig. 527. *Bibiocephala elegantula*, lateral aspect.  
Fig. 528. *Dolichopus bifractus*, lateral aspect.





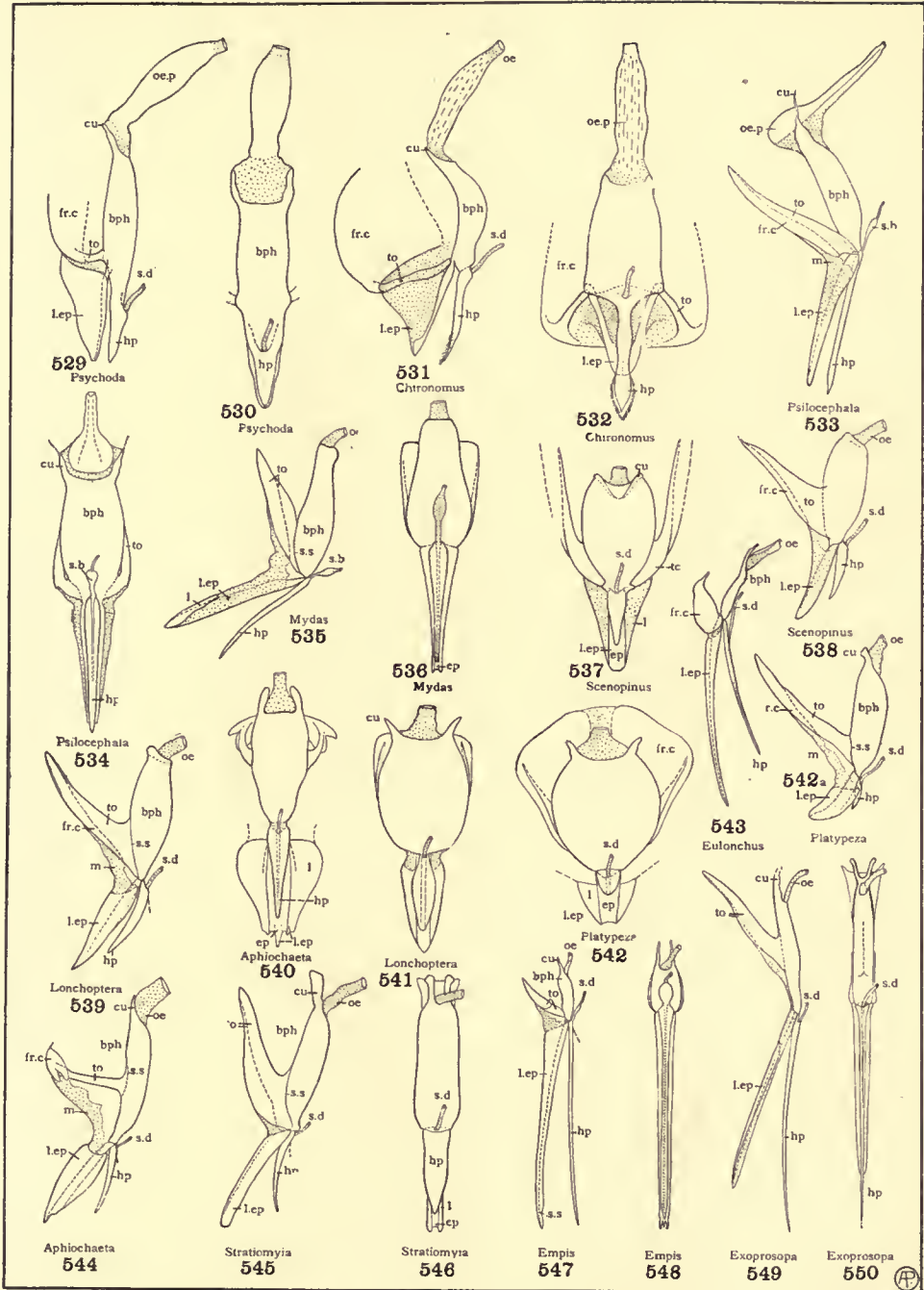


## PLATE XXIII

## EXPLANATION OF PLATE

## EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

- Fig. 529. *Psychoda albipennis*, lateral aspect.  
Fig. 530. *Psychoda albipennis*, caudal aspect.  
Fig. 531. *Chironomus ferrugineovittatus*, lateral aspect.  
Fig. 532. *Chironomus ferrugineovittatus*, caudal aspect.  
Fig. 533. *Psilocephala haemorrhoidalis*, lateral aspect.  
Fig. 534. *Psilocephala haemorrhoidalis*, caudal aspect.  
Fig. 535. *Mydas clavatus*, lateral aspect.  
Fig. 536. *Mydas clavatus*, caudal aspect.  
Fig. 537. *Scenopinus fenestralis*, caudal aspect.  
Fig. 538. *Scenopinus fenestralis*, lateral aspect.  
Fig. 539. *Lonchoptera lutea*, lateral aspect.  
Fig. 540. *Aphiochaeta agarici*, caudal aspect.  
Fig. 541. *Lonchoptera lutea*, caudal aspect.  
Fig. 542. *Platypeza velutina*, caudal aspect.  
Fig. 542a. *Platypeza velutina*, lateral aspect.  
Fig. 543. *Eulonchus tristis*, lateral aspect.  
Fig. 544. *Aphiochaeta agarici*, lateral aspect.  
Fig. 545. *Stratiomyia apicula*, lateral aspect.  
Fig. 546. *Stratiomyia apicula*, caudal aspect.  
Fig. 547. *Empis clausa*, lateral aspect.  
Fig. 548. *Empis clausa*, caudal aspect.  
Fig. 549. *Exoprosopa fasciata*, lateral aspect.  
Fig. 550. *Exoprosopa fasciata*, caudal aspect.







## PLATE XXIV

## EXPLANATION OF PLATE

## EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

- Fig. 551. *Calobata univitta*, caudal aspect.  
Fig. 552. *Calobata univitta*, lateral aspect.  
Fig. 553. *Sapromyza vulgaris*, lateral aspect.  
Fig. 554. *Sapromyza vulgaris*, caudal aspect.  
Fig. 555. *Chloropisca glabra*, caudal aspect.  
Fig. 556. *Chloropisca glabra*, lateral aspect.  
Fig. 557. *Chrysomya demandata*, caudal aspect.  
Fig. 558. *Chrysomya demandata*, lateral aspect.  
Fig. 559. *Coelopa vanduzeei*, caudal aspect.  
Fig. 560. *Coelopa vanduzeei*, lateral aspect.  
Fig. 561. *Pipunculus cingulatus*, caudal aspect.  
Fig. 562. *Pipunculus cingulatus*, lateral aspect.  
Fig. 563. *Drosophila ampelophila*, caudal aspect.  
Fig. 564. *Drosophila ampelophila*, lateral aspect.  
Fig. 565. *Borborus equinus*, lateral aspect.  
Fig. 566. *Borborus equinus*, caudal aspect.  
Fig. 567. *Borborus equinus*, hypopharynx united with labium, caudal aspect.  
Fig. 568. *Chyromya concolor*, caudal aspect.  
Fig. 569. *Chyromya concolor*, lateral aspect.  
Fig. 570. *Loxocera pectoralis*, caudal aspect.  
Fig. 571. *Loxocera pectoralis*, lateral aspect.  
Fig. 572. *Euaresta aequalis*, caudal aspect.  
Fig. 573. *Euaresta aequalis*, lateral aspect.  
Fig. 574. *Ochthera mantis*, lateral aspect.  
Fig. 575. *Ochthera mantis*, caudal aspect of the labrum.  
Fig. 576. *Ochthera mantis*, caudal aspect of the epipharynx.  
Fig. 577. *Ochthera mantis*, caudal aspect.  
Fig. 578. *Desmometopa latipes*, lateral aspect.  
Fig. 579. *Desmometopa latipes*, caudal aspect.

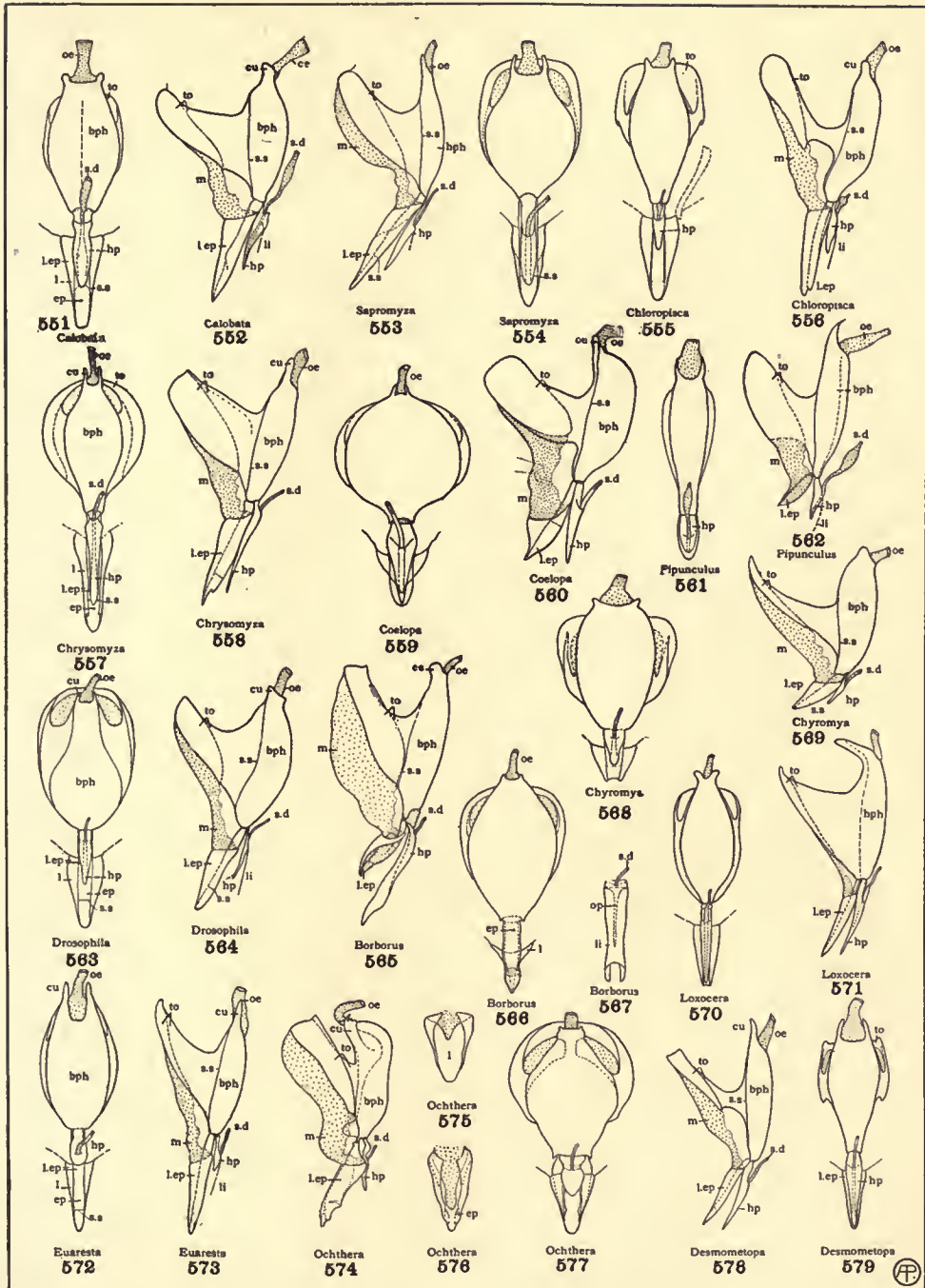




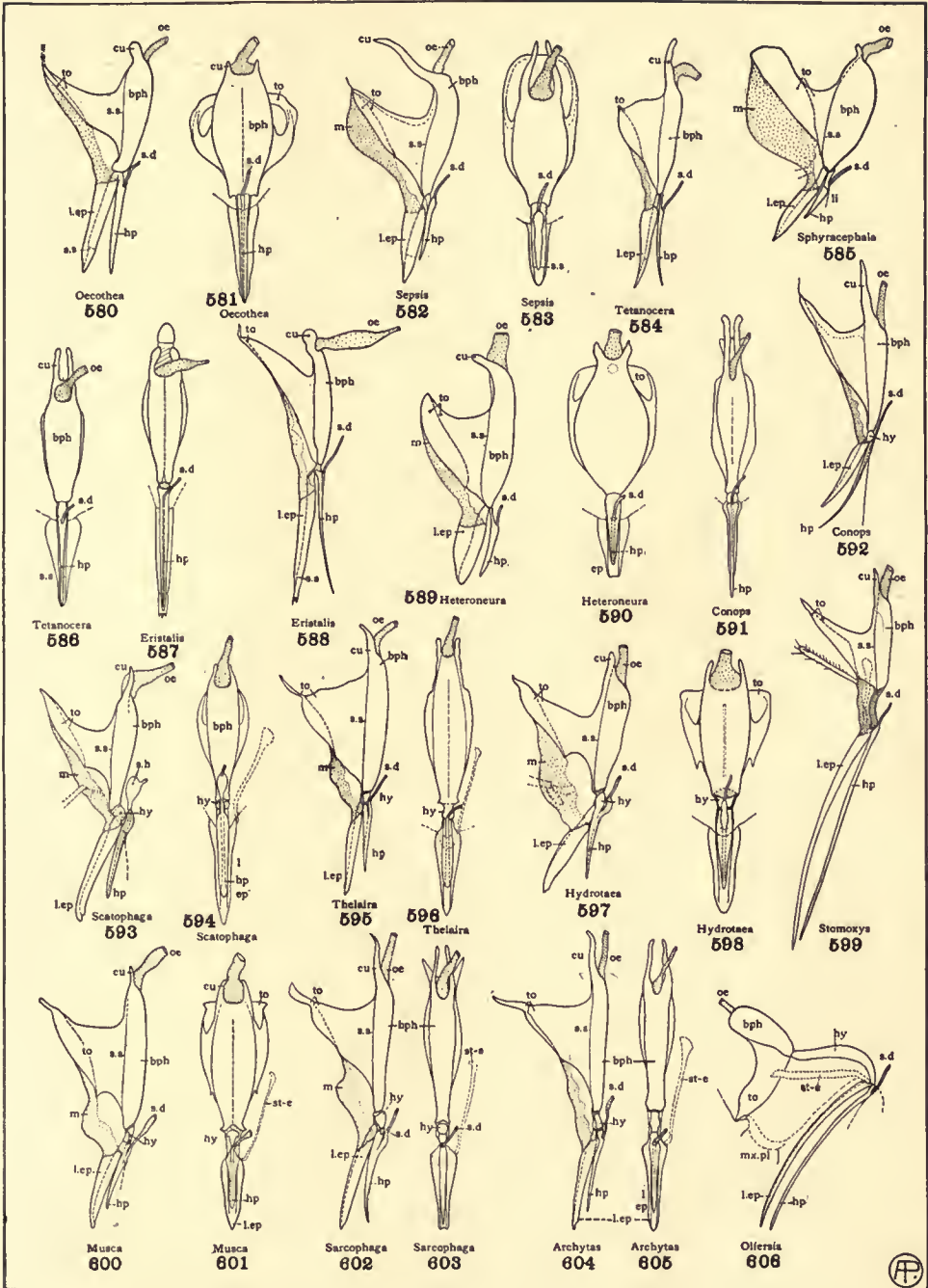
PLATE XXV



## EXPLANATION OF PLATE

## EPIPHARYNX AND HYPOPHARYNX AND ASSOCIATED PARTS

- Fig. 580. *Oecotheca fenestralis*, lateral aspect.  
Fig. 581. *Oecotheca fenestralis*, caudal aspect.  
Fig. 582. *Sepsis violacea*, lateral aspect.  
Fig. 583. *Sepsis violacea*, caudal aspect.  
Fig. 584. *Tetanocera plumosa*, lateral aspect.  
Fig. 585. *Sphyracephala brevicornis*, lateral aspect.  
Fig. 586. *Tetanocera plumosa*, caudal aspect.  
Fig. 587. *Eristalis tenax*, caudal aspect.  
Fig. 588. *Eristalis tenax*, lateral aspect.  
Fig. 589. *Heteroneura flaviseta*, lateral aspect.  
Fig. 590. *Heteroneura flaviseta*, caudal aspect.  
Fig. 591. *Conops brachyrhynchus*, caudal aspect.  
Fig. 592. *Conops brachyrhynchus*, lateral aspect.  
Fig. 593. *Scatophaga furcata*, lateral aspect.  
Fig. 594. *Scatophaga furcata*, caudal aspect.  
Fig. 595. *Thelaira leucozona*, lateral aspect.  
Fig. 596. *Thelaira leucozona*, caudal aspect.  
Fig. 597. *Hydrotaea dentipes*, lateral aspect.  
Fig. 598. *Hydrotaea dentipes*, caudal aspect.  
Fig. 599. *Stomoxys calcitrans*, lateral aspect.  
✓ Fig. 600. *Musca domestica*, lateral aspect.  
Fig. 601. *Musca domestica*, caudal aspect.  
Fig. 602. *Sarcophaga haemorrhoidalis*, lateral aspect.  
Fig. 603. *Sarcophaga haemorrhoidalis*, caudal aspect.  
Fig. 604. *Archytas analis*, lateral aspect.  
Fig. 605. *Archytas analis*, caudal aspect.  
Fig. 606. *Olfersia ardeae*, lateral aspect.













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